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Created in 1849, the United States Department of the Interior—a department of conservation—is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States—now and in the future.

SEXUAL MATURATION AND SPAWNING OF ATLANTIC MENHADEN

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ABSTRACT

This study of the sexual development and incidence spawning of the Atlantic menhaden, *Brevoortia* *rannus* (Latrobe), is based on an examination of aries collected along the Atlantic Coast of the United ates from 1956 to 1959. Description of the distribu- on and developmental stages of ovarian ova was based diameter measurements. Four developmental oups of ova were distinguishable in the ovaries of ar-spawning fish: immature, intermediate, maturing d ripe. Two groups, each in a different stage of aturation, simultaneously developed but it could not determined whether the second group was spawned.

A numerical relation, called the "ovary index," was tablished between the length of the fish and the ight of both ovaries and used to distinguish sexually active and inactive fish. Based on changes in the mean ovary index and numbers of sexually active fish in commercial catches, it was concluded that spawning occurred at different times in different areas of the coast. In the North Atlantic Area, spawning apparently took place during summer; in the Middle Atlantic Area, in spring and again in autumn; and in the South Atlantic Area, during winter.

Most females became sexually mature at age 2, and the estimated number of ova spawned by an individual each season ranged from 38,000 to 631,000 ova.

Seasonal variation in spawning was considered in relation to differential size and age distribution of the fish, seasonal migrations, and population structure.

The life history and biology of the Atlantic enhaden, *Brevoortia tyrannus* (Latrobe), are udied by the Bureau of Commercial Fisheries as rt of a research program to determine causes of riations in the distribution, availability, and undance of this species. Sexual maturation d spawning are among the more important pects of the biology which must be understood interpret such variations. Determination of e time and place of spawning not only may plain seasonal variations in the distribution and ailability of adults, but is fundamental to a udy of the distribution and survival of embryos d larvae. Knowledge of fecundity and of the e and/or age at first spawning may be used to ess the reproductive potential of the spawning ck.

The work had several aims: (1) to describe the acroscopic changes of ovarian ova as they develop to maturity, (2) to develop a method of determining rapidly and objectively the relative maturity of ovaries, (3) to investigate the distribution of near-spawning fish in time and space, (4) to determine the age and size at first spawning, and (5) to estimate the fecundity of fish of different sizes.

COLLECTION AND PRELIMINARY TREATMENT OF OVARIES

Most of the ovaries used in this study were obtained from routine length and age samples taken from purse seine catches landed throughout the fishing season at Portland, Maine; Gloucester, Mass.; Amagansett, N.Y.; Port Monmouth, N.J.; Lewes, Del.; Reedville, Va.; Beaufort-Morehead City, N.C., from 1956 to 1959 (fig. 1). Additional specimens were obtained from pound net catches landed at Port Monmouth and Reedville prior to commencement of the purse seine fishing season

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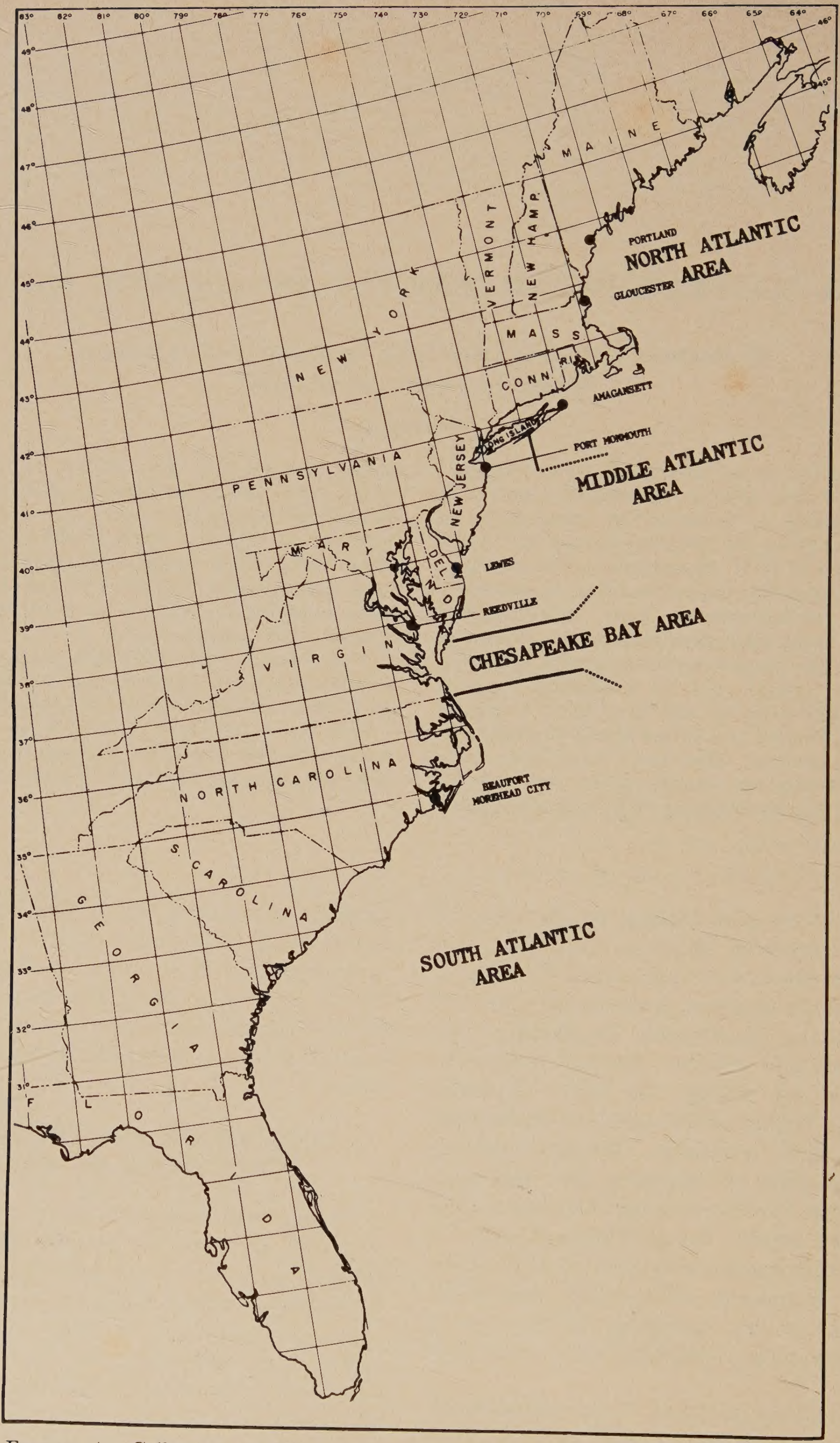
PORTLAND
NORTH ATLANTIC AREA
GLOUCESTER
AMAGANSETT
PORT MONMOUTH
MIDDLE ATLANTIC AREA
LEWES
REEDVILLE
CHESAPEAKE BAY AREA
BEAUFORT
MOREHEAD CITY
SOUTH ATLANTIC AREA
MAINE
VERMONT
NEW HAMP.
MASS
CONN
R.I.
NEW YORK
LONG ISLAND
NEW JERSEY
PENNSYLVANIA
MARY
DEL
MD
VIRGINIA
NORTH CAROLINA
S. CAROLINA
GEORGIA
FLORIDA

FIGURE 1.—Collection localities and areas used in summarizing maturity and spawning data on Atlantic menhaden.

ıd from incidental landings in various localities y otter trawlers. Methods of sampling the ıtch followed those described by June and eintjes (1959).

At the time of collection, both ovaries were moved from each female, weighed to the nearest 1 g., and assigned an arbitrary stage of sexual aturity. In 1956 and 1957, ovaries of the first ve females in each catch sample were labeled, rapped in cheesecloth, and preserved in 10 per-nt formalin. Only those containing ripe ova ere preserved in 1958 and 1959. Arbitrary ages of maturity assigned to ovaries in the field ere:

Stage I. Ovaries small, torpedo-shaped, deep d, and occupying a small fraction of the body vity. Ova invisible to the naked eye.

Stage II. Ovaries red to yellow, occupying oout one-third to one-half of the body cavity. va invisible to the naked eye.

Stage III. Ovaries swollen, yellow, and occu-ying about two-thirds of the body cavity. Ova sible through the ovarian membrane.

Stage IV. Ovaries occupying about three-urths or more of the body cavity. Ova yellow ıd readily separated from the follicles when the varian wall was pressed.

Stage V. Ovaries flabby, bloodshot, and occu-ying less than one-half of the body cavity. ıtact, ripe ova present in the lumen of an ovary.

The primary purposes of examining ovaries and signing arbitrary stages of maturity in the field ere: (1) to insure collection and preservation of l ripe specimens (Stage IV), and (2) to dis-guish recently spent specimens (Stage V), since ter hardening in formalin, the latter usually ere indistinguishable from those in the early aturing stage (Stage II).

Preserved ovary specimens collected in 1956 ıd 1957 were used for detailed study of matura-on. Several specimens containing ripe ova which ere collected and preserved in 1958 and 1959 so were used. Specimens length, and at least ıe specimen, when available, was chosen at ndom from each half-centimeter length class presented in the weekly catch samples at each ort. This method of selection resulted in nearly ual representation of all length and age classes opearing in the catch samples during the 1956 ıd 1957 fishing seasons. Of 3,945 preserved ecimens, 1,030 (26.1 percent) were used for detailed study. During the 1956–59 fishing seasons, ovaries of 37,548 females were examined in the field for determination of stage of maturity.

MEASUREMENT OF OVA FOR MATURITY DETERMINATIONS

The distribution and stages of relative maturity of ova within the ovaries were determined from diameter measurements. Since all preserved ova were not spherical, it was necessary to choose some arbitrary method of measuring their diameters. Two methods were compared. One hundred of the most mature ova in a single ovary first were measured along the axis which, by chance, was parallel to the graduations of an ocular micrometer. The same ova were then measured along the shortest and longest axes and the two measurements averaged (table 1). The variance of the mean of single measurements was 4.27 and of two measurements, 1.48. Single measurements, however, were made in one-third the time required for two measurements. Thus, for expediency, all ova subsequently were measured once along whatever axis fell parallel to the ocular micrometer

TABLE 1.—*Comparison of measurements of random diameters and the mean of maximum and minimum diameters of 100 ova from a single ovary (specimen 3.3583), in micrometer units* [1]

Random diameter	Mean diameter	Random diameter	Mean diameter	Random diameter	Mean diameter
35	33.0	31	31.5	34	34.0
33	33.0	31	34.0	33	34.5
34	34.0	34	35.0	32	33.0
35	35.0	39	24.5	35	35.5
38	34.5	35	34.0	37	36.0
36	35.5	32	34.0	39	36.0
32	32.5	34	35.5	37	35.5
32	35.0	33	34.5	36	34.5
33	33.5	38	35.0	33	36.5
34	35.0	35	34.5	37	35.5
33	34.5	38	36.5	37	34.5
39	36.0	35	36.0	33	34.0
34	34.0	36	35.0	35	35.0
34	24.5	34	35.0	34	33.5
37	35.5	33	32.5	38	33.0
33	33.0	38	36.0	31	34.0
34	34.0	34	33.5	33	34.5
33	34.0	35	34.5	32	34.0
35	32.5	34	36.0	34	32.0
35	35.0	36	36.5	35	34.0
30	33.0	33	31.5	37	35.0
31	32.5	30	34.5	36	35.5
32	32.5	37	35.5	33	34.5
34	31.5	35	35.5	39	36.5
33	32.0	35	36.0	32	35.0
33	32.5	36	35.0	35	34.0
32	33.5	36	35.0	35	34.0
35	33.0	34	36.5	35	34.0
34	33.5	32	34.5	36	36.0
35	33.5	32	34.0	34	35.0
32	32.5	34	33.5	35	35.0
33	33.5	35	35.5	37	34.5
35	34.0	35	34.0		
35	35.5	38	34.0		
Mean				34.49	34.36
Variance				4.27	1.48

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[1] One micrometer unit equals 0.033 mm.

TABLE 2.—*Diameter-frequency distributions of maturing ova in samples from various locations within a single ovary (specimen 0.10812)*

[P=Periphery; M=Mid-section; I=Interior]

Diameter	Location								
	Anterior			Central			Posterior		
	P	M	I	P	M	I	P	M	I
Millimeters	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
0.73	2	2	2	1	---	2	---	1	
.76	2	1	3	4	3	---	---	---	
.79	1	5	5	9	8	5	3	7	
.82	12	16	13	11	12	6	5	13	
.86	10	12	19	22	15	23	16	16	1
.89	20	28	23	26	21	27	26	13	2
.92	27	34	40	22	21	36	22	24	2
.96	31	24	33	35	12	26	32	31	4
.99	28	21	30	19	36	40	35	34	3
1.02	19	13	13	15	11	17	19	25	1
1.06	14	6	7	4	12	17	12	9	
1.09	4	7	2	2	5	4	7	5	
1.12	5	1	2	3	2	1	2	3	
1.16	1	2	2	4	4	1	5	3	
1.19	---	2	1	---	2	2	1	1	
1.22	---	---	---	---	---	---	1	3	---
1.25	---	---	---	---	---	---	1	---	---
Total	176	174	195	177	164	207	187	188	20
Mean diameters (mm.)	0.95	0.94	0.93	0.93	0.95	0.95	0.96	0.96	0.9
Weight of sample (g.)	.084	.088	.94	.088	.082	.092	.094	.084	.09

graduations. This method has been applied by other investigators (Clark, 1934; June, 1953; Schaefer and Orange, 1956; Yuen, 1955) and was judged to be sufficiently precise in the present study.

Different areas within a single ovary of a pair were sampled to determine if the maturing ova were distributed uniformly. A cross section, approximately 1 millimeter (mm.) thick, was cut from the anterior, central, and posterior parts and a wedge removed from each section. Each wedge was divided into three parts, corresponding to the periphery (*P*), mid-section (*M*), and interior (*I*), and a subsample of approximately 0.09 g. taken. Diameters were measured and counts were made of all maturing ova in each of the nine subsamples and the results (table 2) analyzed statistically. Neither the differences in mean diameters, nor the differences in numbers were significant at the 95 percent level.

Comparisons also were made of the mean diameters and numbers of mature ova in samples from the central portions of the right and left ovary (table 3). A *t*-test showed no significant difference in mean ova diameters; however, a statistically significant chi-square value ($P<0.01$) resulted from comparison of the numbers of ova. Inspection of the data showed discrepancies in the 0.82, 1.02, and 1.06 mm. size classes, but since the frequency distributions otherwise appeared similar, it was judged that there were n biological differences in ova from the right an left ovary.

TABLE 3.—*Diameter-frequency distributions of maturin ova in samples from the right and left ovary of a singl fish (specimen 6.7012)*

Diameter	Right ovary	Left ovary
Millimeters	*Number*	*Number*
0.73	11	
.76	11	
.79	41	
.82	94	1
.86	138	1
.89	204	2
.92	259	2
.96	255	2
.99	290	2
1.02	154	1
1.06	101	
1.09	47	
1.12	21	
1.16	23	
1.19	15	
1.22	4	
1.25	1	
Total	1,669	1,5
Mean diameter (mm.)	0.95	0.

Ova that were measured to establish the matur ty stage of the preserved specimens were obtaine by cutting a cross section from the central portio of the right ovary and removing a small wedg The wedge was placed on a glass slide, and th ova were teased from the follicular tissues b dissecting needles with the aid of a binocul microscope. Parallel guidelines etched on th glass minimized the chance of measuring the sam ovum more than once. Diameter measurements vere made to the nearest ocular micrometer unit 0.017 mm.). If a specimen contained only immature ova (<0.18 mm.), measurements of about 00 ova were considered adequate to establish his stage of development. If larger ova were present, generally from 200 to 300 of the most nature ova were measured to delineate their size listribution.

DESCRIPTION OF THE OVARIES

Ovaries of Atlantic menhaden are paired, elonated organs suspended from the dorsal wall of he abdominal cavity by the mesovarium. They re elliptical in cross section and separate from ach other, except where the two oviducts unite osteriorly before entering the cloaca. The right vary usually is slightly larger than the left. Ovaries of sexually immature fish are deep red, orpedo-shaped, and may measure no more than everal millimeters in length. They are similar n appearance to the testes, but are distinguishable y the oocytes which can be clearly seen under agnification, even in recently metamorphosed uveniles. As females develop to maturity, their varies increase in length and girth, and become rm and pale yellow. At the approach of spawng, the ovaries become distended, occupying two-irds or more of the abdominal cavity; the periphral blood vessels become enlarged; and the ova are isible through the ovarian membrane. Following pawning, the ovaries are flaccid and bloodshot, nd residual ova occur in the follicular tissues and the lumina.

DEVELOPMENTAL STAGES OF OVARIAN OVA

One or more distinct groups of ova are recogzable in the ovaries of an individual fish at one me or another throughout the year, depending n the proximity of spawning. Based on the ppearance and diameters of formalin-preserved aterial, these may be described as follows:

mmature

Ova which are transparent, irregular in shape, nd which contain relatively large, eccentric uclei. These range from less than 0.02 mm. to pproximately 0.22 mm. in diameter and average 11 mm. These are present in great numbers nd comprise the oocytes from which smaller umbers of ova periodically mature (fig. 2).

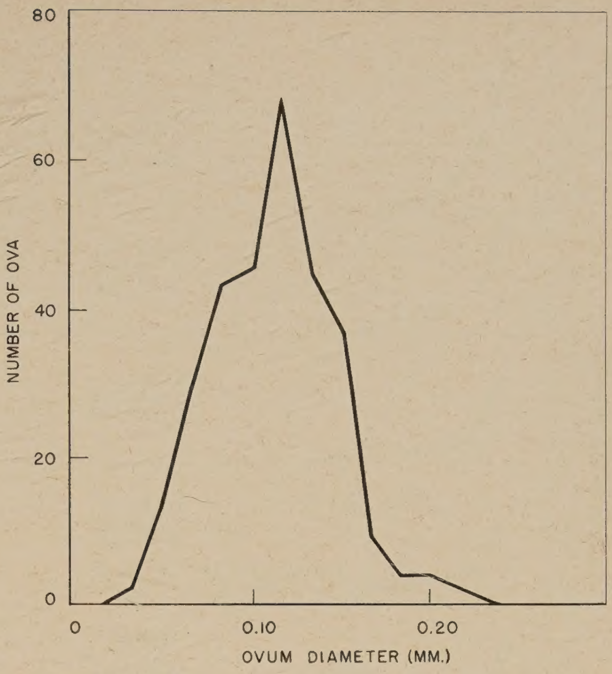

Figure 2.—Frequencies of ovum diameter of 300 immature ova from an Atlantic menhaden (specimen 2.1483).

Intermediate

Ova which are semiopaque, spherical, and in which the nuclei have become obscure due to the deposition of yolk granules in the cytoplasm. These range from approximately 0.18 to 0.34 mm. in diameter and are barely visible without magnification.

Maturing

Ova which are opaque and yellow due to abundant yolk material. These range from approximately 0.35 to 0.78 mm. in diameter and are clearly visible within the follicles.

Ripe

Ova which are translucent, each with a single, yellow oil globule, from 0.10 to 0.19 mm. in diameter. Ripe ova range from approximately 0.79 to 1.33 mm. in diameter. They readily burst from the follicles when the ovarian wall is pressed and sometimes are found lying loosely in the lumen of an ovary.

The four developmental groups of ova are present in the ovaries of all near-spawning fish. Development to maturity of ova within the ovaries of a single fish, with no connotation of time, is illustrated in figure 3. The percentage frequencies of ova-diameter measurements of several specimens were grouped into six arbitrary

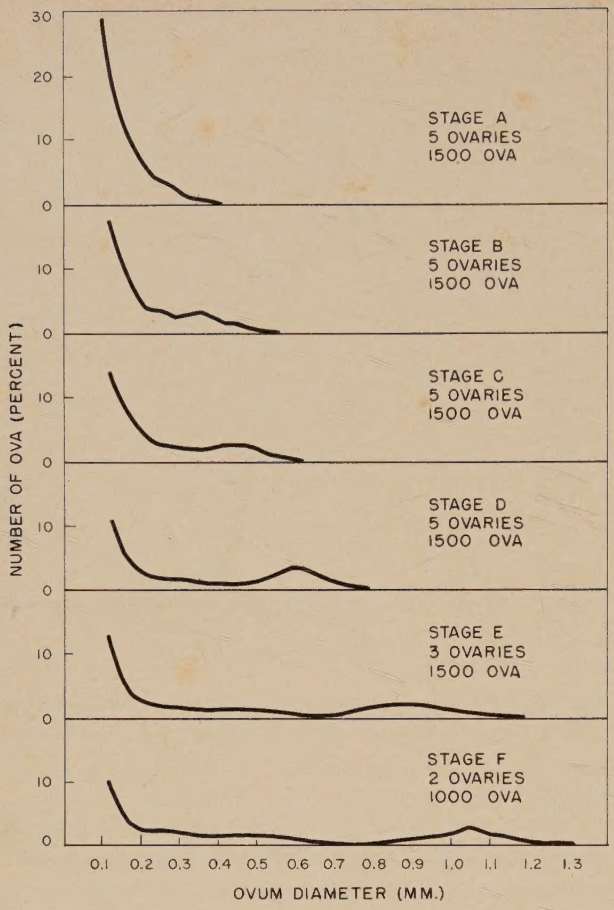

FIGURE 3.—Frequencies of ovum diameter showing the development to maturity. (The data were classified into six arbitrary stages according to the mode of the most mature group of ova. The smallest immature ova were not measured.)

stages, based on the mode of the most mature group, and smoothed twice by a moving average of three. Only ova larger than 0.12 mm. were included. A mode representing ova which eventually would ripen during a single spawning season was first discernible at 0.27 mm. (stage A). It became more sharply defined at 0.36 and 0.48 mm. (stages B and C) and distinct at 0.63 (stage D). The mode at approximately 0.90 mm. (stage E) represented semitranslucent ova which, on the basis of size, had become almost separated from the preceding groups. Ripe ova, ranging from 0.86 to 1.33 mm., with a mode at 1.08 mm. (stage F), constituted a distinct group and were nearly ready to be extruded. A second group of developing ova, between approximately 0.34 and 0.68 mm., was distinguishable by the time that the most advanced group became semitranslucent (stage E).

OVARY SIZE AS A MEASURE OF MATURITY

Many workers have used ova-diameter measurements to characterize the relative sexual maturity of the ovaries of individual fish (Brock, 1954; Clark, 1934; Thompson, 1915). This method, however, is laborious, and where large numbers o fish are examined, some simpler, objective method usually is desirable. Changes in ovary weight i relation to body size as the ovaries develop t maturity have been used in spawning studies o a number of species (Farran, 1938; Masterman 1913a and 1913b; Olsen and Merriman, 1946) Later investigators (June, 1953; Schaefer and Orange, 1956; Yuen, 1955) related the size o ovarian ova to the weight of the ovaries and size of the fish and established indices of maturity which ultimately could be computed from ovary weight and fish size.

In the present study, the relation between ova diameters and an "ovary index" was examined i

TABLE 4.—*Ovary indices of 1, 030 specimens containing ovarian ova in various stages of development*

Ovary index	Developmental stage of the most mature ovarian ova				Total
	Immature	Inter-mediate	Matur-ing	Ripe	
	Number	*Number*	*Number*	*Number*	*Number*
<1.0	150	16			16
1.0–1.9	145	202			34
2.0–2.9	12	82	2		9
3.0–3.9		14	6		2
4.0–4.9			42		4
5.0–5.9			39		3
6.0–6.9			31		3
7.0–7.9			46		4
8.0–8.9			28		2
9.0–9.9			19		1
10.0–10.9			21	1	2
11.0–11.9			20		2
12.0–12.9			24		2
13.0–13.9			16		1
14.0–14.9			9		
15.0–15.9			18		1
16.0–16.9			14	1	1
17.0–17.9			18	2	2
18.0–18.9			7	1	
19.0–19.9			13		1
20.0–20.9			9	1	1
21.0–21.9			6	1	
22.0–22.9			3		
23.0–23.9			2		
24.0–24.9			3	2	
25.0–25.9					
26.0–26.9					
27.0–27.9			1		
28.0–28.9					
29.0–29.9				1	
30.0–30.9					
31.0–31.9					
32.0–32.9					
33.0–33.9					
34.0–34.9				1	
Total	307	314	398	11	1,0

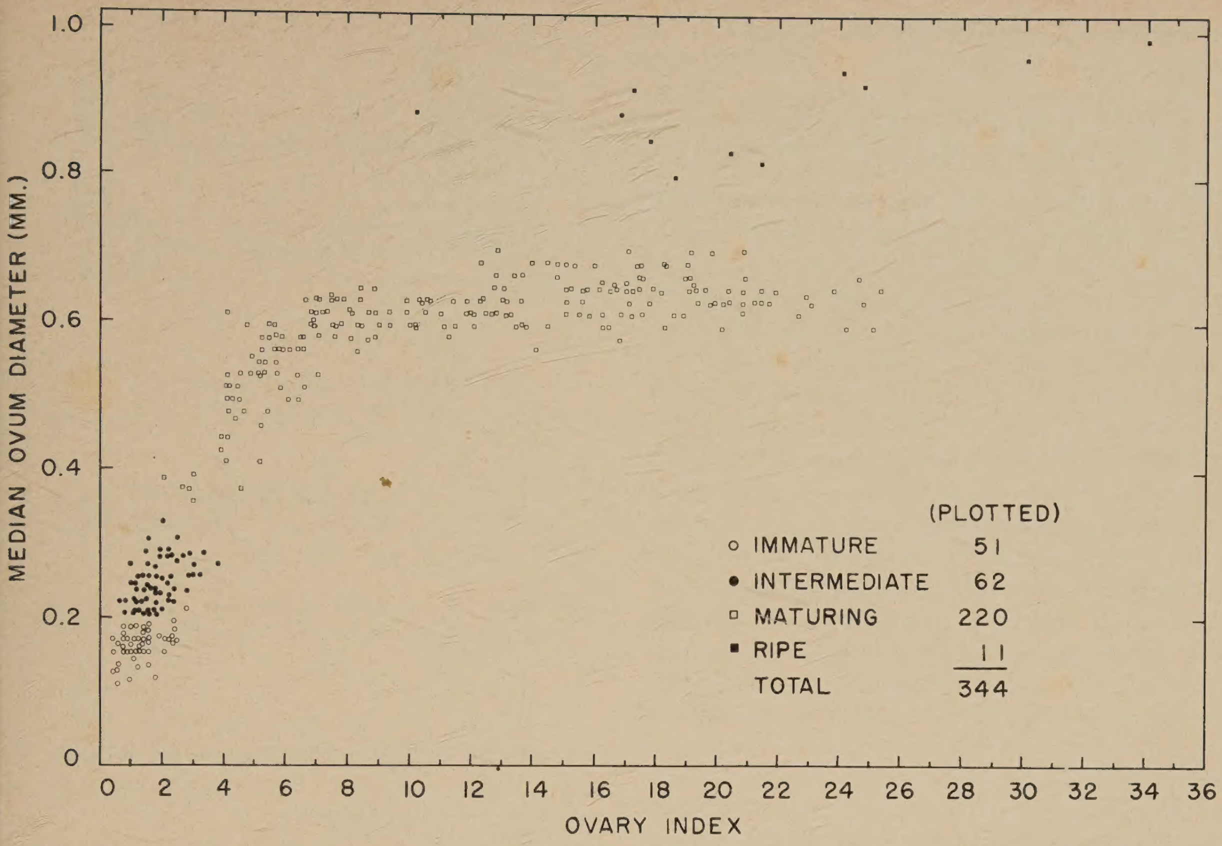

FIGURE 4.—Relation between ovary index and median of diameter frequency distributions of the most mature group of ova in 344 specimens.

1,030 specimens. The index was computed from the formula: $O.I.=\frac{W\times10^{7}}{L^{3}}$

where $O.I.$=ovary index
W=weight of both ovaries in grams
L=fork length of the fish in millimeters [1]

Of 621 specimens which contained only immature or intermediate ova (<0.34 mm. in diameter), 607 (97.7 percent) had an ovary index of less than 3, and the remainder had an index of less than 4 (table 4). Indices of 409 specimens which contained maturing and ripe ova ranged from 2.9 to 34, and all but eight of these (2.0 percent) had an index greater than 4. In figure 4, the median of the ova-diameter frequency distributions of the most mature ova was plotted against the corresponding ovary index. The relation increased linearly up to an ovum diameter of about 0.60 mm., changed abruptly, and then tended to level off. The ovary index of 11 specimens which contained ripe ova, however, varied between 10 and 34, and there appeared to be a definite relation between the size of the most advanced ovarian ova and the ovary index.

From the foregoing, it was concluded that there was reasonably good agreement between the ovary index and the size of ovarian ova. Thus, the ovary index provided a simple, objective means of distinguishing ovary specimens which were approaching spawning. Since relatively few ripe and recently spent ovaries were found in the commercial catches, a more precise measure of sexual maturity was superfluous. Ripe ovaries were readily distinguishable by the fact that ova flowed freely from the oviduct with the slightest pressure on the ovaries. Recently spent ovaries also were easily distinguished by their flaccid, bloodshot appearance, and most of these yielded an ovary index of three or less. Verification was made by the presence of intact, ripe ova in the lumina of the ovaries.

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[1] In Atlantic menhaden, body weight is nearly proportional to the cube of the length.

PLACE AND TIME OF SPAWNING INFERRED FROM OVARY INDICES

The geographical and seasonal distribution of spawning was inferred from ovary indices on the assumption that females with an index of 4.0 or more would have actively spawned somewhere in the vicinity of capture. For convenience, those with an index of 4.0 or more were classified as "active" and those with an index of less than 4.0, as "inactive." Females with an index of less than 4.0 whose ovaries were hollow, flaccid, bloodshot, and contained some intact, ripe ova were classified as "spent." The resulting data were summarized by four major geographical areas described by June and Reintjes (1959) and shown in figure 1. The numbers of females classified according to the above criteria are listed by area, month, and year in table 5. In figures 5, 6, and 7 the percentage frequencies of sexually active females are shown by month and year for the North, Middle, and South Atlantic Areas. The mean ovary index also is plotted on these figures.

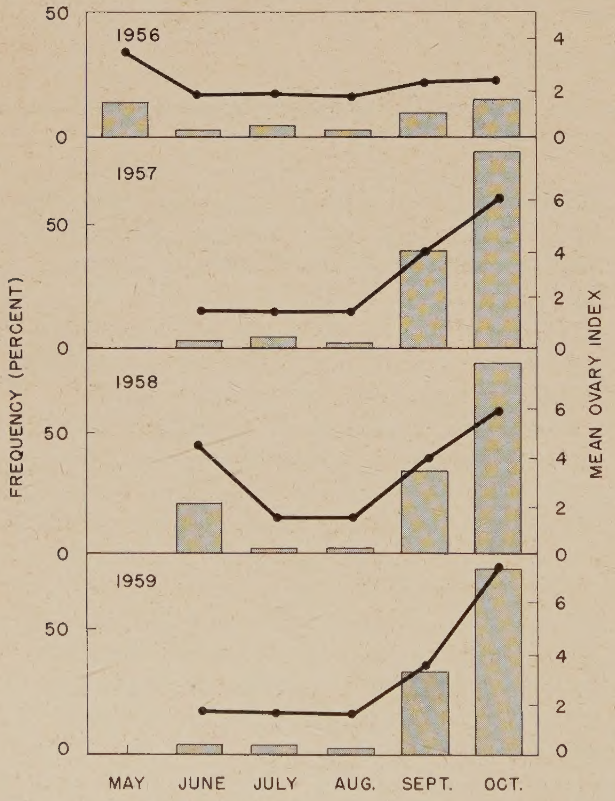

FIGURE 5.—Frequencies of sexually active females and mean ovary indices, by month and year, North Atlantic Area, 1956–59.

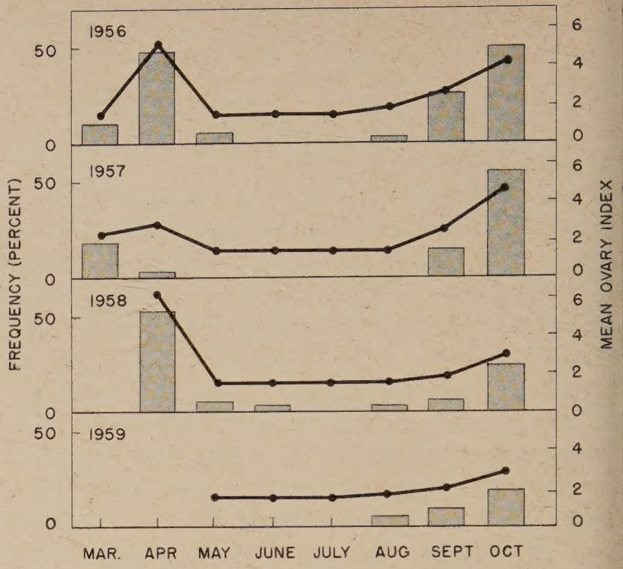

FIGURE 6.—Frequencies of sexually active females and mean ovary indices, by month and year, Middle Atlantic Area, 1956–59.

Because so few ripe and recently spent specimens were collected (only 11 specimens containing numerous ripe ova were encountered in the routine field examination of several hundred thousand fish during 4 years of sampling), it was not possible to determine the time required for ova of sexually active fish to become fully ripe and extruded. Hence, it is possible that spawning occurred in some locality other than where sexually active females were caught. The paucity of both ripe and recently spent specimens and the occurrence of numerous collections which consisted entirely of sexually active females suggests, however, that Atlantic menhaden change their habits so as to become unavailable to the fishery prior to and following spawning. Whether spawning fish segregate in schools or in smaller groups is unknown.

NORTH ATLANTIC AREA

Atlantic menhaden were caught by purse seines in northern coastal waters from June to October in every year; consequently most of our collections were limited to this period. A few specimens were obtained from pound nets in May 1956. Ovaries of 6,511 females were ex-

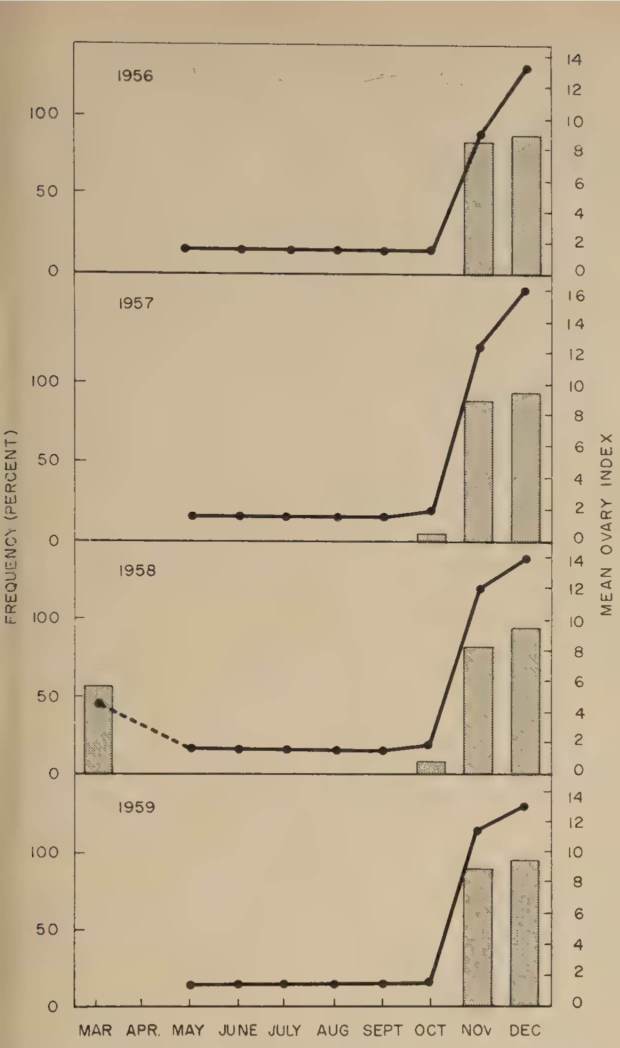

FIGURE 7.—Frequencies of sexually active females and mean ovary indices, by month and year, South Atlantic Area, 1956–59.

amined between 1956 and 1959. Active and/or spent females were represented in every month for which there were data (table 5 and figure 5). Many of the specimens obtained in May 1956 and n June 1958 were active and had high ovary ndices. In most years, however, the numbers of active fish in June, July, and August constituted only a small fraction of the monthly totals, and the mean ovary index increased in September and reached a maximum in October. It was oncluded from these data that spawning took lace in the North Atlantic during the entire eriod that the fish were available to the fishery, nd reached a peak in October.

The above conclusions agree with published eports of the occurrence of planktonic eggs and larvae. Kuntz and Radcliffe (1917) found both eggs and larvae in the vicinity of Woods Hole, Mass., in June, July, August, and again in October. Herman (1959) reported the occurrence of eggs and larvae in Narragansett Bay from May to August and again in October and concluded that there was a split spawning season in that locality, the autumn spawning being the most productive. Perlmutter (1939) reported eggs and larvae in northern Long Island waters from May to September, and Richards (1959) and Wheatland (1956) concluded that spawning took place in Long Island Sound from May to October, with peaks occurring in early summer and in autumn.

MIDDLE ATLANTIC AREA

A pound net fishery for Atlantic menhaden operates off New Jersey and southern Long Island beginning in April and is followed by the purse seine fishery beginning in May. The purse seine fishery continues until October when the fish disappear from the coastal waters (June and Reintjes, 1959). Except during mild winters, when occasional catches are made by pound nets and otter trawls, the fish are not known to occur in concentrations inshore until the following March or April.

Ovaries of 14,749 females were examined from March to October during the 4-year period (a few specimens were obtained in December 1957). Active and spent females occurred in substantial numbers in April, but abruptly decreased in May (table 5 and figure 6). Only 12 active or spent females appeared in the catches in June, July, and August. In every year, the number of active fish increased in September and generally reached a maximum in October. The mean ovary index was high in April, remained low during the summer, but increased again in September and October. It appears from these data that spawning occurred in spring and again in autumn, with possibly very limited spawning during the summer. The main spawning season was indicated to be in autumn.

There are no published reports of the occurrence of planktonic eggs and larvae within the area; however, evidence that spawning takes place in spring and autumn comes from numerous plankton collections of larvae taken at Indian River Inlet, Del. Routine sampling was conducted at this location

TABLE 5.—*Number of sexually inactive, active, and spent female Atlantic menhaden in catch samples, by area and month, 1956–59*

Area, year, and ovary condition	Month										Total
	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
North Atlantic:											
1956:											
Inactive				323	671	573	200	102			1,869
Active			6	2	22	8	22	29			89
Spent			36	11	21	43	12	53			176
1957:											
Inactive				199	600	494	128	19			1,440
Active				4	16	9	91	135			255
Spent					1	3	2	12			18
1958:											
Inactive				65	285	299	166	18			833
Active				19	2	1	98	84			204
Spent					9		17	3			29
1959:											
Inactive				279	427	418	235	17			1,376
Active				8	17	9	106	75			215
Spent				5		2					7
Subtotal:											
Inactive				866	1,983	1,784	729	156			5,518
Active			6	33	57	27	317	323			763
Spent			36	16	31	48	31	68			230
Middle Atlantic:											
1956:											
Inactive	1	144	429	865	484	590	286	211			3,010
Active	1	218	1			1	92	213			526
Spent	9	94	67	4			3	1			178
1957:											
Inactive		61	205	765	813	757	407	281		9	3,298
Active	5	37	1				51	337			431
Spent	24	138	22				1				185
1958:											
Inactive		6	179	576	765	810	794	70			3,200
Active		61	9	4		3	24	21			122
Spent		52	25	2							79
1959:											
Inactive			137	813	984	1,056	549	108			3,647
Active						4	46	23			73
Spent											
Subtotal:											
Inactive	1	211	950	3,019	3,046	3,213	2,036	670			13,155
Active	6	316	11	4		8	213	594			1,152
Spent	33	284	114	6			4	1			442
Chesapeake Bay:											
1956:											
Inactive		32	316	369	438	370	156	39			1,720
Active											
Spent											
1957:											
Inactive		310	79	346	436	434	329	156			2,090
Active		2									2
Spent											
1958:											
Inactive			35	428	430	256	374	110			1,633
Active											
Spent											
1959:											
Inactive			72	455	495	448	479	272	39		2,260
Active											
Spent											
Subtotal:											
Inactive		342	502	1,598	1,799	1,508	1,338	577	39		7,703
Active		2									2
Spent											
South Atlantic:											
1956:											
Inactive			359	446	424	524	230	188	52	38	2,261
Active									273	251	524
Spent											
1957:											
Inactive			385	473	339	178	101	80	40	10	1,606
Active								4	276	204	484
Spent											
1958:											
Inactive			279	300	241	93	210	61	39	44	1,267
Active	50							4	186	316	556
Spent	38										38
1959:											
Inactive			262	371	246	213	81	45	33	15	1,266
Active									243	347	590
Spent											
Subtotal:											
Inactive			1,285	1,590	1,250	1,008	622	374	164	107	6,400
Active	50							8	978	1,118	2,154
Spent	38										38

from 1955 to 1961 as part of an estuarine study conducted by the Menhaden Program. Neither eggs nor larvae were taken in July, August, and September. Larvae appeared in the collections in October, increased in number thereafter, and generally reached a peak of abundance in January. The smallest larvae occurred in the October samples. Their length increased in November, but thereafter remained relatively constant until April when both smaller and larger larvae occurred in the collections (Pacheco, Unpublished Ms.).[2] These findings suggest the following hypotheses: (1) following a period of no spawning in the area throughout the summer, spawning begins in September or October; (2) larvae from the autumn spawning increase in length through November, but subsequently do not grow appreciably until April or May; and (3) smaller larvae which appear in the collections in April result from a spring spawning in the area, while the larger larvae represent the progeny from the previous autumn spawning. The occurrence of sexually active fish in autumn, their absence in the coastal waters during winter, and their reappearance in spring support these hypotheses.

CHESAPEAKE BAY AREA

In Chesapeake Bay, Atlantic menhaden are caught in quantity by pound nets beginning in April (McHugh, 1960). The purse seine fishery begins in late May and usually continues through October, at which time most of the fish apparently disappear from the Bay (June and Reintjes, 1959). Of 7,705 females examined between April and November, only two active specimens were found, both in April 1957 (table 5). No spent females were found. It was concluded, therefore, that spawning probably did not occur in Chesapeake Bay during the period considered.

Kuntz and Radcliffe (1917) were of the opinion that there were two spawning seasons in the Chesapeake Bay area, but offered no data to support their belief. Hildebrand and Schroeder (1928) reported that females with "well-developed" (although not ripe) ovaries were taken in autumn and that larvae were caught from January to April. These authors concluded that spawning occurred in autumn. Pearson (1941) obtained "a limited number" of eggs in late summer and several 20–24 mm. larvae in April and May plankton samples taken in lower Chesapeake Bay and concluded that some spawning probably occurred outside the area of collection during the winter. McHugh, Oglesby, and Pacheco (1959) found no fully mature fish in samples from pound net and purse seine catches, although some specimens approaching maturity were observed in early spring.[3] They further reported that no eggs were found in numerous plankton hauls in Chesapeake Bay; however, larvae 24 to 30 mm. in length were taken as early as April and appeared in greatest abundance in late April and early May. Massmann, Norcross and Joseph (1962) obtained larvae from November to May during monthly offshore plankton cruises in Virginia waters. The smallest specimens were taken in November and ranged between 7 and 10 mm. Those taken during the winter months were fairly uniform in size and ranged from 12 to 29 mm., while those taken in May were larger and ranged between 25 and 33 mm.

The foregoing evidence supports the present conclusion that spawning does not occur in Chesapeake Bay. It is probable that the larvae reported within Chesapeake Bay resulted from an autumn and winter spawning offshore.

SOUTH ATLANTIC AREA

In the South Atlantic Area, Atlantic menhaden are caught exclusively by purse seines, generally from May to December or January.[4] The summer fishery apparently is based on local stocks and usually lasts from about mid-May to mid-October (June and Nicholson 1964). In November, large, migratory schools appear off the coast of North Carolina and support an intense fishery until mid-December when they disappear off Cape Fear, N.C. (June and Reintjes, 1959).

Examination was made of 8,592 specimens obtained from the purse seine fishery and from incidental catches made by otter trawlers. No active females appeared in the catches from May to September in any year, and only eight active females were found in October (table 5 and figure 7). With the appearance of migrating schools in

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[2] Catches of postlarval Atlantic menhaden, *Brevoortia tyrannus*, at Indian River, Delaware. Unpublished Manuscript, U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.

[3] While no sexually active fish were found in the present study from 1956–59, specimens examined in 1955 showed the presence of 1 sexually active fish in May, 1 in September, and 22 in October. Only inactive fish were found in June, July, and August.

[4] Catches in January consist almost exclusively of young-of-the-year fish (age 0) which are sexually immature. These were excluded from the study.

November and December, the number of active females increased abruptly. Eighty-nine percent of the females examined in November and 95 percent of those examined in December were active. The particularly high ovary indices in November and December also indicated that most of the females in the fishable population were in spawning condition. Among 88 specimens collected on an exploratory fishing cruise in March 1958, 50 were active and 38 were spent.

Reintjes (1961) reported the occurrence of eggs and/or newly hatched larvae, principally in the vicinity of Capes Fear and Lookout, N.C., and Cape Kennedy, Fla., from November to March, but none were found during other months of the year. Based on the known distribution of adults, he believed those taken off the North Carolina coast were Atlantic menhaden, while those taken off central Florida were Atlantic menhaden or yellowfin menhaden (*B. smithi*).

Corroborative evidence of continuous spawning off the North Carolina coast from late fall to early spring is furnished from routine plankton collections taken in the vicinity of Beaufort, N.C., from 1955 to 1961 (Unpublished data, Menhaden Program, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.). Eggs and larvae have been collected in the ocean only during the late fall and winter months; however, eggs have not been taken at any time in samples at Beaufort Inlet. In every year, larvae appeared in Beaufort Inlet samples beginning in November or early December, were present continuously thereafter until early or mid-April, and reached a peak of abundance in late February or early March. Larvae in the early December samples invariably were small, ranging from approximately 10 to 20 mm. in length. Samples throughout the winter contained mixed sizes, indicating successive waves of spawning in nearby waters. The largest larvae usually occurred in the April samples. Larvae were never taken from May to November.

It was concluded that spawning occurred in the South Atlantic Area from mid-November to late March, with a peak probably occurring sometime in mid-winter. Based on the concentrations of sexually active fish and the abundance of newly hatched larvae, it is likely that waters off the North Carolina coast are one of the major spawning grounds for Atlantic menhaden.

AGE AND LENGTH AT FIRST MATURITY

Females were considered immature if their ovaries were in the inactive stage (ovary index <4.0) and ova remnants were not found in the follicular tissues or in the lumina. Fish whose ovaries were either active (ovary index>4.0) or in the spent stage, with intact, ripe ova present in the lumina, were considered sexually mature. On the basis of these criteria, little difficulty was experienced in distinguishing sexually mature individuals.

No sexually active age–0 fish (June and Roithmayr, 1960; June and Reintjes, 1959) were found. This age group, therefore, was not considered further. In most years a few mature females of age 1 occurred in catch samples in the Middle Atlantic Area in October; nine females, ranging from 240 to 265 mm. in length, were found in 1956; two, 215 and 235 mm., in 1957; and one, 210 mm., in 1959 (table 6). Greater numbers were found during the fall fishery in the South Atlantic Area. Between October and December (table 7), 22 mature females, ranging from 205 to 260 mm., were found in 1956; one 190-mm. specimen in 1957; 52 specimens, ranging between 180 and 280 mm., in 1958; and two specimens, 200 and 205 mm., in 1959. No mature females in this age group were found in samples from other areas in any year. From these data, it was concluded that some Atlantic menhaden attained maturity at age 1, and these ranged from approximately 180 to 280 mm. in length. The mean lengths indicate that there was a size difference at which females reached maturity in the two areas. There also was a tendency for the mature females

TABLE 6.—*Relation of age, length, and spawning condition of Atlantic menhaden, Middle Atlantic Area, September and October, 1956–59*

Year and age group	Inactive			Active		
	Number	Fork length		Number	Fork length	
		Range	Mean		Range	Mean
		Millimeters	*Millimeters*		*Millimeters*	*Millimeters*
1956:						
Age 1	158	195–265	225.2	9	240–265	248.4
Age 2	127	235–300	260.7	121	235–305	263.2
1957:						
Age 1	339	185–255	209.2	2	215–235	225.0
Age 2	306	195–305	253.7	98	210–320	266.6
1958:						
Age 1	0	--------	--------	0	--------	--------
Age 2	838	215–280	248.4	43	250–280	264.2
1959:						
Age 1	437	165–230	194.3	1	210	210.0
Age 2	91	210–280	241.5	23	235–285	257.6

TABLE 7.—*Relation of age, length, and spawning condition of Atlantic menhaden, South Atlantic Area, October–December, 1956–59*

Year and age group	Inactive			Active		
	Number	Fork length		Number	Fork length	
		Range	Mean		Range	Mean
		Millimeters	*Millimeters*		*Millimeters*	*Millimeters*
1956:						
Age 1	270	140–230	169.3	22	205–260	232.5
Age 2	3	200–235	220.0	100	225–305	265.0
1957:						
Age 1	66	150–210	182.9	1	190	190.0
Age 2	58	180–220	196.4	121	185–315	279.8
1958:						
Age 1	135	170–280	198.1	52	180–280	217.4
Age 2	9	195–240	212.2	253	185–300	261.5
1959:						
Age 1	75	130–225	160.7	2	200–205	202.5
Age 2	9	185–250	210.6	114	210–290	259.0

of age 1 to be the larger individuals within the age group in both areas.

In every year, mature females of age 2 were found in catch samples in the Middle and North Atlantic Areas beginning in September. By October, 48 percent of all females in this age group examined during the 4-year period had attained maturity, and these ranged between 225 and 320 mm. in length. In the South Atlantic Area, 97 percent of the females examined from October through December during the 4-year period were mature, and these ranged from 195 to 315 mm. in length. Thus it would appear that most females mature by age 2. All females of age 3 and older ages were found to be mature. Ovaries of the latter age groups which were examined microscopically, without exception, contained ova remnants from a previous spawning. These findings, in general, agree with those of Westman and Nigrelli (1955) who stated that all females at age 3 and some at age 2 appeared to be mature.

FREQUENCY OF SPAWNING DURING A SEASON

The frequency distribution of ova diameters in figure 3 showed that, within the ovaries of Atlantic menhaden, there was a progression to maturity of one group of advanced ova, distinguished by a single, well-defined mode. This was followed by a second group of developing ova which became clearly discernible by the time the mode of the first group had advanced to about 0.90 mm. In the lower three panels of the figure (stages D–F), it may be seen that ova constituting the second group continued to increase in size as the first group advanced to maturity. Thus, it appears that at least two groups of ova develop within a single spawning season, but the question arises as to whether the second matures and is spawned in the same season.

Because so few females in a ripe or near-ripe condition were available in the fishable population, there was no way of determining the fate of the secondary group of ova. A few specimens were collected which had high ovary indices and contained intact, ripe remnants in the lumina. These ovaries were turgid, contained numerous near-ripe ova, and appeared to be ready to spawn in the near future. Recently spent ovaries contained relatively few intermediate and maturing ova in the follicular tissues. Furthermore, the yolk granules of intermediate and maturing ova which remained in the follicular tissues of recently spent ovaries collected in spring were speckled, and the ova were dark, distorted, and appeared to be disintegrating. Yolk granules of the numerous developing ova in specimens taken in late summer and early autumn were globular, and the ova were spherical (cf. Intermediate ova, p. 259). Finally, the absence of remnants within follicular tissues in latent ovaries of sexually mature fish during the summer indicates that residual intermediate and maturing ova are not carried over to the following spawning season. From available evidence, it is impossible to decide conclusively the frequency of spawning by individual fish. We favor, however, the hypothesis of the maturation and fractional spawning of more than one group of ova during a single season.

NUMBER OF OVA SPAWNED

The number of ova assumed to be extruded from the most advanced group of ovarian ova was estimated for 38 fish which ranged in length from 203 to 346 mm. A sample from each ovary specimen was weighed to the nearest 0.001 g. Ova were teased from the follicular tissues and those classified as maturing (p. 259) were counted. The number of maturing ova in both ovaries was estimated by multiplying the number in the sample by the ratio of the weight of both ovaries to the weight of the sample (table 8). The number of ova per female varied widely, but increased with length. Individual estimates ranged from 38,000 to 631,000 ova. A plot of the estimated number

TABLE 8.—*Estimated number of ova in the most advanced group in ovaries of fish of different sizes*

Fork length	Fish weight	Weight of both ovaries	Sample weight	Number of maturing ova in sample	Estimated number of maturing ova in pair of ovaries
Millimeters	*Grams*	*Grams*	*Gram*		*Thousands*
203	167	7.1	0.179	1,266	50
204	157	7.3	.178	1,439	59
208	174	6.9	.159	1,036	45
211	174	6.8	.174	1,292	50
216	184	5.6	.189	1,295	38
221	221	12.3	.205	1,525	92
228	234	15.2	.182	1,348	113
240	269	14.5	.237	1,161	71
243	281	19.4	.283	1,642	113
244	280	10.3	.232	1,299	58
246	290	15.5	.222	1,261	88
247	283	7.3	.278	1,852	49
251	295	25.4	.209	1,113	135
258	327	23.6	.290	1,967	160
259	322	14.2	.217	1,715	112
267	346	32.6	.196	1,383	230
270	368	26.3	.165	1,278	204
274	443	41.9	.216	1,135	220
278	368	27.6	.279	1,788	177
278	446	45.1	.113	793	316
285	441	35.2	.412	2,753	235
285	413	37.1	.161	1,194	275
290	536	42.3	.292	2,005	290
299	572	39.9	.118	1,230	416
305	619	54.0	.194	1,485	413
309	661	44.8	.346	2,546	330
313	543	50.0	.189	921	244
313	579	41.1	.356	2,665	308
317	646	62.8	.142	977	432
317	651	46.6	.173	1,012	272
327	750	40.2	.167	1,208	291
328	637	55.4	.334	3,452	573
333	732	74.3	.102	594	433
336	771	68.9	.206	1,536	514
339	910	62.8	.183	1,071	368
343	848	89.0	.174	1,042	533
345	858	78.9	.194	1,551	631
346	786	81.5	.209	1,438	561

of ova on fish length (figure 8) gave a relation which is curvilinear.

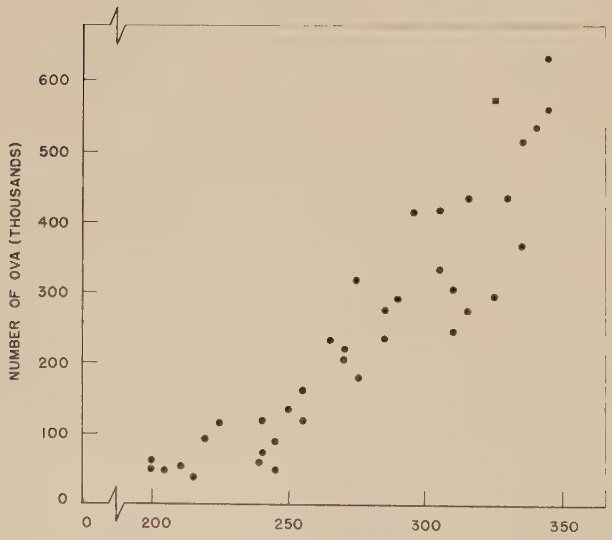

FIGURE 8.—Relation between fish length and the estimated number of maturing ova.

Suttkus and Sundararaj (1961) reported on the fecundity and reproduction of Gulf menhaden, *B. patronus*. This species reaches maturity younger and at a smaller size than *B. tyrannus*. The number of ova produced, for fish of comparable size, is greater in the former species.

DISCUSSION

The seasonal variations in spawning in different areas of the coast may be explained by seasonal variations in the distribution of age and size classes of fish. June (1961), June and Nicholson (1964), and June and Reintjes (1959 and 1960) have shown that during the summer, the purse seine catch in the North Atlantic Area is composed mostly of age-3 and older fish, whereas fish of ages 1 and 2 dominate the catches in other areas. Since all females were found to be sexually mature at age 3, it would be expected that any spawning during the summer would be limited to the North Atlantic Area. Based on the occurrence of dominant length-age groups, June and Nicholson (1964) postulated a cyclic north-south migration of at least a portion of the population north of Chesapeake Bay—southward in autumn and northward in spring. Such a migration pattern would account for the occurrence of the older, sexually mature fish (many of which are in spawning condition) in the Middle Atlantic Area in September and October and again in March, April, and May, and probably accounts for the appearance of sexually mature fish (most of which are in spawning condition, p. 259) in the South Atlantic Area in November and December. Apparently not all fish migrate southward in autumn, however, since numerous inactive and recently spent females occurred in the catches in the North and Middle Atlantic Areas in September and October (table 5). They also are known to have occurred in the latter area during the winter, yet very few inactive, and no spent females appeared in the catches in the South Atlantic Area in November and December. Although the time required for sexually inactive ovaries to become active is unknown, it seems unlikely that maturation would occur over a period of about 2 weeks—the time interval between the disappearance of schools from surface waters in the Middle Atlantic Area and the reappearance of schools off the North Carolina coast. The almost complete absence of inactive females among the older, sexually mature fish which appear in large schools in the latter area in November and December would suggest that the southward migration in autumn is primarily a spawning migration.

The hypothesis of a cyclic north-south migration of spawning fish would explain the observed variations in the time and space distribution of sexually active fish, eggs, and larvae. According to this hypothesis, spawning during the summer is restricted to the North Atlantic Area where older, sexually mature fish are largely confined. Beginning in September, there is an increase in the number of active fish followed by a general movement southward during which spawning occurs. These migrating schools are joined by other sexually active fish in the Middle Atlantic Area, and spawning continues as the schools move southward. In some seasons, these large schools of sexually active fish are followed as far southward as Delaware and northern Maryland by the purse seine fleet, and the appearance of eggs and larvae in the coastal waters of Delaware and Virginia (p. 265) coincides with the occurrence of such schools in these latitudes. Eventually the schools disappear from the surface waters (sometime in late October), but reappear several weeks later off the coast of North Carolina. Spawning occurs in the South Atlantic Area through the winter. Some individuals continue spawning during the return northward migration in spring as both sexually active and recently spent specimens appear along with sexually inactive specimens in pound net catches along the Middle Atlantic coast in March, April, and May. The older, sexually mature fish finally return to the summer grounds north of Long Island, N.Y. Thus, it is possible that those fish which were sexually inactive in the previous autumn, and which may not have joined in the southward migration, spawn in northern waters during the summer.

The above hypothesis also could account for the variation in meristic characters of juvenile Atlantic menhaden inhabiting estuarine nurseries reported by June (1958) and Sutherland (1963). These authors found that juveniles of five successive year classes were separable into two groups or subpopulations, one occurring north and the other south of Long Island. They also showed that variations in meristic numbers were associated with seasonal differences in water temperatures on the spawning grounds, and Sutherland concluded that the relative stability of the meristic pattern suggested genetic origin. Our data suggest that the fish which spawn in waters north of Long Island in summer constitute a distinct group, which becomes segregated from that which migrates southward and spawns in the South Atlantic Area in winter. If this is indeed the case, it is likely that differences in the physiological condition of individuals, hence differences in the time of year at which their gonads develop to spawning, have a genetic basis. It also would be expected that some overlap in spawning would occur in the vicinity of Long Island where individuals of these two spawning groups apparently segregate in autumn and intermingle again in the following spring during the return migration into northern waters.

Variations in fecundity of females of comparable size (fig. 8) and age suggest that differences in the size and age at attainment of sexual maturity (p. 266) should be explored further, since these may yield further insight into the question of genetic differences in physiology between these two apparent spawning groups. Along these lines, further study of spawning fish in Florida waters is necessary to determine if they differ from those farther northward.

SUMMARY

Ovaries of Atlantic menhaden (*Brevoortia tyrannus*) were obtained during routine sampling of catches at seven ports along the Atlantic Coast of the United States during four fishing seasons, 1956–59. Ovaries were weighed and examined at the time of sampling. Some were preserved for further laboratory study.

Preliminary studies indicated that diameter-frequency distributions of ova sampled in different parts of a pair of ovaries were similar. One or more developmental groups of ova were distinguishable within the ovaries, depending on the nearness of spawning; these were immature, intermediate, maturing, and ripe. Plots of ova-diameter frequency distributions showed the simultaneous development of more than one group of ova within the ovaries of an individual fish.

A relation, called the "ovary index," was calculated between fish length and the weight of both ovaries and compared to the medians of the diameter frequency distributions of the most mature group of ova in 1,030 specimens. Although the ovary index did not completely correct for the effect of fish length on the weight of ovaries containing ova in the same stage of development, it could be used reasonably well to distinguish inactive ovaries from those which were advancing toward spawning.

Time of spawning in four geographical areas was inferred from ovary indices. Spawning apparently occurred in the North Atlantic Area from May to September; in the Middle Atlantic, from March through May and again in September and October; and in the South Atlantic, from October through March. There was little evidence that spawning occurred inside Chesapeake Bay.

Few females were found to be mature at age 1 (180–280 mm., fork length); most were mature at age 2 (195–320 mm., fork length); and all were mature at age 3 (over 200 mm. fork length).

Simultaneous maturation of two groups of ova within the ovaries suggests that an individual female may spawn more than one group of ova during a single season; however, no conclusions were reached since there was no way of determining the fate of the secondary group. Extrusion of ova appears to be fractional.

Assuming that ova comprising the most advanced group are extruded, estimates of the number of ova spawned during spawning season, ranged from 38,000 to 631,000, depending on the length of the fish.

Variation in times and places of spawning and attainment of first maturity appear to be related to the differential distribution of age and size groups, seasonal migrations, and population structure.

LITERATURE CITED

Brock, Vernon E.

1954. Some aspects of the biology of the aku, *Katsuwonus pelamis*, in the Hawaiian Islands. Pacific Science, vol. 8, No. 1, pp. 94–104.

Clark, Frances N.

1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. California Division of Fish and Game, Fish Bulletin No. 42, 49 pp.

Farran, G. P.

1938. On the size and number of the ova of Irish herrings. Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil, vol. 13, No. 1, pp. 91–100.

Herman, Sidney S.

1959. The planktonic fish eggs and larvae of Narragansett Bay. Appendix I. U.S. Fish and Wildlife Service, Sustaining data summary on fishery resources in relation to the hurricane damage control program for Narragansett Bay and vicinity Rhode Island and Massachusetts. (May 1959) Boston, Mass., 24 pp.

Hildebrand, Samuel F., and William C. Schroeder.

1927. The fishes of Chesapeake Bay. Bulletin of the U.S. Bureau of Fisheries, vol. 43, part 1, (1928) 366 pp.

June, Fred C.

1953. Spawning of yellowfin tuna in Hawaiian waters. U.S. Fish and Wildlife Service, Fishery Bulletin 77, vol. 54, pp. 47–64.

1958. Variation in meristic characters of young Atlantic menhaden, *Brevoortia tyrannus*. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 143, part 2, No. 4, pp. 26–35.

1961. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1957; with a brief review of the commercial fishery. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 373, 39 pp.

June, Fred C., and William R. Nicholson.

1964. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1958; with a brief review of the commercial fishery. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 446, 40 pp.

June, Fred C., and John W. Reintjes.

1959. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1952–55; with a brief review of the commercial fishery. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 317, 65 pp.

1960. Age and size composition of the menhaden catch along the Atlantic Coast of the United States, 1956; with a brief review of the commercial fishery. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 336, 38 pp.

June, Fred C., and Charles M. Roithmayr.

1960. Determining age of Atlantic menhaden from their scales. U.S. Fish and Wildlife, Service, Fishery Bulletin 171, vol. 60, pp. 323–342.

Kuntz, Albert, and Lewis Radcliffe.

1917. Notes on the embryology and larval development of twelve teleostean fishes. Bulletin of the U.S. Bureau of Fisheries, vol. 35, for 1915–16, pp. 87–134.

Massmann, William H., John J. Norcross, and Edwin B. Joseph.

1962. Atlantic menhaden larvae in Virginia coastal waters. Chesapeake Science, vol. 3, No. 1, pp. 42–45.

Masterman, A. T.

1913a. Report on investigations upon the salmon with special reference to age-determination by study of scales. Board of Agriculture and Fisheries. Fishery Investigations, series 1, vol. 1, No. 1, pp. 3–111.

1913b. Report on investigations upon the smelt (*Osmerus eperlanus*) with special reference to age-determination by study of scales and its bearing upon sexual maturity. Board of Agriculture and Fisheries. Fishery Investigations, series 1, vol. 1, No. 2, pp. 113–126.

McHugh, J. L.

1960. The pound-net fishery in Virginia. Part 2. Species composition of landings reported as menhaden. U.S. Fish and Wildlife Service, Commercial Fisheries Review, vol. 22, No. 2 (February), pp. 1–16.

McHugh, J. L., R. T. Oglesby, and A. L. Pacheco.

1959. Length, weight, and age composition of the menhaden catch in Virginia waters. Limnology and Oceanography, vol. 4, No. 2, pp. 145–162.

lsen, Yngve H., and Daniel Merriman.

1946. Studies on the marine resources of southern New England. The biology and economic importance of the ocean pout, *Macrozoarces americanus* (Bloch and Schneider). Bulletin of the Bingham Oceanographic Collection, vol. 9, art. 4, 184 pp.

earson, John C.

1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout, *Cynoscion regalis* (Bloch). U.S. Fish and Wildlife Service, Fishery Bulletin 36, vol. 50, pp. 79–102.

erlmutter, Alfred.

1939. An ecological survey of young fish and eggs identified from tow-net collections. *In* A biological survey of the salt waters of Long Island, 1938, part 2, pp. 11–71. New York State Conservation Department, supplemental to 28th annual report, 1938.

Reintjes, John W.

1961. Menhaden eggs and larvae from M/V *Theodore N. Gill* cruises, South Atlantic Coast of the United States, 1953–54. U.S. Fish and Wildlife Service. Special Scientific Report—Fisheries No. 393, 7 pp.

Richards, Sarah W.

1959. Oceanography of Long Island Sound. VI. Pelagic fish eggs and larvae of Long Island Sound. Bulletin of the Bingham Oceanographic Collection, vol. 17, art. 1, pp. 95–124.

Schaefer, Milner B., and Craig J. Orange.

1956. Studies of the sexual development and spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the Eastern Pacific Ocean, by examination of gonads. Bulletin of the Inter-American Tropical Tuna Commission, vol. 1, No. 6, pp. 281–349.

Suttkus, Royal D., and Bangalore I. Sundararaj.

1961. Fecundity and reproduction in the largescale menhaden, *Brevoortia patronus* Goode. Tulane Studies in Zoology, vol. 8, No. 6, pp. 177–182.

Sutherland, Doyle F.

1963. Variation in vertebral numbers of juvenile Atlantic menhaden. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 435, 21 pp.

Thompson, William F.

1915. A preliminary report on the life-history of the halibut. Report of the British Columbia Commissioner of Fisheries for 1914, pp. N76–N99.

Westman, James R., and Ross F. Nigrelli.

1955. Preliminary studies of menhaden and their mass mortalities in Long Island and New Jersey waters. New York Fish and Game Journal, vol. 2, No. 2, pp. 142–153.

Wheatland, Sarah B.

1956. Oceanography of Long Island Sound, 1952–1954. VII. Pelagic fish eggs and larvae. Bulletin of the Bingham Oceanographic Collection, vol. 15, pp. 234–314.

Yuen, Heeny S. H.

1955. Maturity and fecundity of bigeye tuna in the Pacific. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 150, 30 pp.

AN EXPERIMENTAL EVALUATION OF THE C ^{14} METHOD FOR MEASURING PHYTOPLANKTON PRODUCTION, USING CULTURES OF *DUNALIELLA PRIMOLECTA* BUTCHER [1]

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ABSTRACT

The photosynthetic uptake of radioactive carbon
lioxide was compared with net and gross O_2 production,
H changes, and growth in cultures of *Dunaliella*
rimolecta Butcher. During the logarithmic growth
hase of such cultures, C^{14} uptake agreed well with net
$_2$ production and did not differ greatly from gross O_2
roduction. The logarithmic growth rate of mass
ultures (measured by increases in cell concentration,
ptical density, dry weight, organic carbon and nitrogen)
as generally less than a similar logarithmic rate cal-
ulated from organic carbon analyses and measurements
f photosynthesis in bottles immersed in the culture.
his difference was attributed to greater illuminances
n the bottles than in the cultures as a whole. In one
xperiment, when illumination conditions were similar,
he two rates were equivalent.

When cultures were incipiently nitrogen-deficient, C^{14} uptake was similar to net O_2 production and growth was equivalent to photosynthesis. In one experiment, when nitrogen deficiency was extreme, C^{14} uptake was larger than net O_2 production, and agreed more closely with gross O_2 production. In another such experiment, C^{14} uptake agreed with net O_2 production. Nitrogen deficiency increased the intracellular C/N ratio, and starch became a major storage product. In one experiment, C^{14} uptake in an incipiently phosphorus-deficient culture was intermediate between net and gross O_2 evolution; in a similar experiment, C^{14} uptake was less than net O_2 production. C^{14} uptake in healthy cultures was equivalent to the uptake of CO_2 as measured by pH changes. These results are discussed in relation to other findings and to oceanographic applications.

It is commonly accepted that in the open sea
he production of all forms of animal life is ulti-
iately dependent upon the production of organic
iaterial by phytoplankton. The phytoplankton
roduce organic material in excess of their meta-
olic needs, and this excess or "net production"
then available to other forms of life. This ex-
ess consists mainly of protein, carbohydrate, and
pid fractions. This material forms the bulk of
e food available for incorporation into the cells
d tissues of the zooplankton and larval fishes
econdary producers), and also provides an energy
urce for their activities. Ideally, to study the
namic aspects of the transfer of food from
hytoplankton to secondary producers, it would
desirable to measure changes in the concentrations of protein, carbohydrate, and lipid in the sea, or at least, to measure changes in total phytoplankton biomass. Practically, such measurements are very difficult, because present methods are either quite time-consuming or are too insensitive to measure the small changes that occur in the sea.

Since the three major components of phytoplankton all contain carbon, the development of the C^{14} method for measuring the production of organic carbon (Steemann Nielsen, 1952), ap-

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peared to provide a sensitive and easy way of measuring changes in the food supply, if the C^{14} method really measures the excess or net production. Intensive investigations of the spatial and temporal variations of C^{14} assimilation that are now in progress should therefore contribute to our understanding of food production in the oceans, and may provide information of practical importance to fishermen. The quantitative determination of phytoplankton production in the sea may also allow a more precise assessment of the effects of various factors on production and of the manner in which it is controlled. Thus, it is rather important that this method be subjected to a detailed evaluation.

To determine phytoplankton photosynthesis with C^{14}, a sample of water containing phytoplankton is placed in a clear, glass-stoppered bottle to which a standard amount of $Na_2C^{14}O_3$ is added as a tracer. The sample is then incubated for a standard length of time either in situ, under known conditions of illumination and temperature, or under conditions which simulate field conditions. Following incubation, the algae are collected on a membrane filter and dried carefully. Their assimilated C^{14} is then counted. The amount of carbon assimilated during the photosynthetic period is calculated from the measured assimilation of tracer carbon, the amount of tracer added, and the total CO_2 content of the water (cf. formula on page 12). The methodology of using C^{14} has been discussed by Steemann Nielsen (1952), Ryther (1956), and Doty and Oguri (1958); and has been reviewed in great detail by Strickland (1960). Thomas (1963) reviewed the various physiological factors which affect the measurement.

So far, the C^{14} method has been tested mainly by comparison of C^{14} uptake with O_2 evolution (Ryther, 1954; Ryther and Vaccaro, 1954; Ryther, 1956; Steemann Nielsen and Al Kholy, 1956; Ichimura and Saijo, 1958). One comparison of the C^{14} method with increases in algal biomass (growth) has been made (McAllister, Parsons, Stephens, and Strickland, 1961). This comparison utilized a natural population enclosed in a plastic bag.

Growth is a net process; for the biomass of algae to increase, material which is produced must be conserved in excess of respiratory requirements. Herbivores utilize the algal material directly for food. Algal growth measurements provide a direct assay of the increase in available food. Thus, ideally, the C^{14} method should be compared with growth.

The present paper reports comparisons of C^{14} measurements with increases of phytoplankton solids and of organic carbon in rapidly growing cultures of *Dunaliella primolecta* Butcher and also in incipiently nitrogen- and phosphorus-deficient cultures. Further comparisons of O_2 evolution and C^{14} uptake under varying conditions of intracellular nutrient status are presented. CO_2 assimilation by healthy cultures, as measured by pH changes, is also compared with C^{14} uptake.

MATERIALS AND METHODS[2]

THE ALGA

The organism used in these studies was *D. primolecta* Butcher, which was obtained from Beatrice Sweeney of the Scripps Institution of Oceanography. According to Luigi Provasoli (personal communication) and to Butcher (1959), this alga was originally isolated by Gross, and is now number 81 in the Culture Collection of the Marine Biological Association at Plymouth, England. According to Robert Guillard (personal communication), *D. euchlora*, which was used by Ryther (1954, 1956), is a separate species.

CULTURE PROCEDURES

Stock cultures were maintained on agar slants made with a medium similar to that of Sweeney and Hastings (1957), which consisted of 75 percent sea water, 0.1 percent Na_2EDTA,[3] 2 percent soil extract, 2,000 µg.-at. KNO_3/1., and 200 µg.-at. K_2HPO_4/1. Subcultures used in each experiment consisted of 50-ml. liquid cultures of the same medium. Stock cultures and the liquid subcultures were grown routinely at 500 foot-candles (ft.-c.) and 21° C. Culture methods used in the individual experiments are described below.

Growth of cultures in most experiments was measured by cell counting. A 10-ml. aliquot of the suspension was first treated with a few drops of Lugol's iodine solution to kill and stain the cells. Subsamples from this 10-ml. aliquot were then placed in the chambers of a hemocytometer, and the cells were counted until a total of at least

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[2] Reference to a company or product throughout this manuscript does not imply approval by the U.S. Bureau of Commercial Fisheries.

[3] Na_2EDTA is the sodium salt of ethylene diamine tetraacetic acid.

200 cells had been counted. The standard error of the mean count of these subsamples ranged rom ±2 to ±33 percent. The average standard rror was ±13 percent.

In some experiments, growth was also measured by determinations of dry weight and optical lensity. For dry-weight determinations, aliquots of the cell suspension were filtered through tared HA Millipore ® filters (pore size 0.45 μ), which were dried at room temperature in a vacuum lesiccator. Optical density determinations were nade at 600 and 650 mμ with a Bausch and Lomb Spectronic 20 ® Spectrophotometer and 1-inch bsorption tubes.

Growth is expressed in terms of logarithmic rowth rate constants using the formula (Krauss nd Thomas, 1954):

$$K_2 = \frac{\log_2 C_2 - \log_2 C_1}{t_2 - t_1}$$

where C_1 and C_2 are cell numbers, dry weights, ptical densities, or other growth measurements t times t_1 and t_2. The reciprocal of K_2 is the ime taken for the population to double and is lesignated the "generation time" in this paper.

CARBON ^{14} METHODS

The C^{14} method used is similar to that described by Steemann Nielsen (1952), Ryther (1956), and thers. The radioactive solution was prepared by cidifying $BaC^{14}O_3$ in vacuo and absorbing the resulting $C^{14}O_2$ in NaOH solution. This solution vas then diluted, and the pH was adjusted to pH .5–10.0. The diluted solution contained 1 μc./ml. nd was packaged in ampoules, which were then terilized in the autoclave.

The solution was standardized by precipitating he C^{14} as $BaC^{14}O_3$ and filtering portions of the resulting suspension through HA Millipore ® filters pore size 0.45μ). With the standardization procedure described by Steemann Nielsen (1952), it vas difficult to obtain reproducible radioactivities t low thickness of precipitate (<0.5 mg./cm.²), lthough thicker preparations were quite reproducible. Therefore, the following modifications vere introduced to make thin samples more reproducible: 1) the amount of carrier sodium carbonate uggested by Steemann Nielsen was reduced by ne-half; 2) the filters were washed with 0.001 nolar $BaCl_2$ to avoid losses of precipitate; 3) the $BaC^{14}O_3$ suspension was stirred with a magnetic stirrer during precipitation and sampling; and 4) the filter was shaken during filtration to distribute the precipitate uniformly on the surface of the filter.

Self-absorption curves obtained using these modifications are shown in figure 1. For windowless counting, the values were empirically extrapolated to zero thickness (solid line in curve A, fig. 1) and the error of this value was approximately ±5 percent. Thicknesses of $BaC^{14}O_3$ as low as 0.05 mg./cm.² were used in the extrapolation. Jitts and Scott (1961) have criticized on various grounds our extrapolation from thicknesses below 0.4 mg./cm.². Though their criticisms may be valid, an empirical extrapolation to zero thickness activity using low thicknesses (<0.4 mg./cm.²) results in a value that is about 13 percent higher than that found by using thick samples alone (dashed lines in curve A, fig. 1). Their

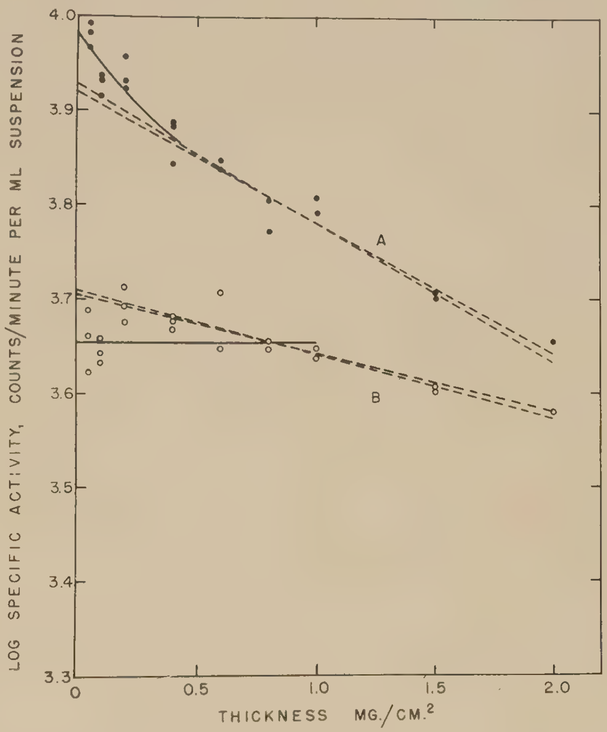

FIGURE 1.—$BaC^{14}O_3$ self-absorption curves: (A) Samples counted with a windowless flow chamber; and (B) samples counted with a chamber fitted with a Mylar window of approximately 1 mg./cm.² thickness. Broken lines show the extrapolation to zero thickness using thick samples (≧0.4 mg./cm.² in curve A; ≧0.2 mg./cm.² in curve B). Solid lines show the empirical extrapolations that were actually used to determine zero-thickness activity.

liquid scintillation method results in a zero-thickness value that is 17–26 percent higher than that obtained by extrapolation from thick pads. Thus, our empirical method of extrapolation gives zero-thickness activities which do not differ greatly from the liquid scintillation values obtained by Jitts and Scott.

Using a counting chamber fitted with a Mylar window, we found a slight decrease in specific activity (cpm/ml.) as the thickness approached zero (open circles, fig. 1). This decrease was observed in three separate standardizations and may be due to a decrease in "self-scattering" of the beta radiation, as suggested by Steinberg and Udenfriend (1957). Since this effect does not occur when the same pads are counted with a windowless chamber, it is probably related to scattering of those beta particles having energies great enough to allow them to pass the window. Despite the downward trend of specific activity at very low thicknesses, at thicknesses below 1 mg./cm.^{2} these specific activities do not differ significantly from each other. Thus, a mean of specific activities obtained at thicknesses below 1 mg./cm.^{2} was taken to be that added to the experimental bottles. This mean had a standard error of ±4 percent and is shown by the solid line of curve B, figure 1. It was about 11 percent less than that obtained by extrapolation from thick samples (dashed lines in curve B).

For C^{14} measurements of photosynthesis in laboratory cultures, 50-ml. portions of the cell suspension were placed in 67-ml. bottles. In some experiments where the cell suspension was very dense, 10-ml. portions of the suspension were diluted to 50 ml. with sterile sea water. The bottles were then inoculated with 1 ml. of C^{14} solution. They were prepared in duplicate and incubated for periods not exceeding 6 hours (generally 1–2 hours). Darkened bottles and illuminated bottles were always incubated together. Bottles were darkened by wrapping them with aluminum foil.

Following incubation, the contents of the bottles were filtered through membrane filters (pore size 0.45μ), and the filters were washed four times with 10- to 20-ml. portions of nonradioactive sea water. The filters were then dried in a vacuum desiccator at room temperature.

The radioactivity on the filters was measured with a proportional flow counter using either a windowless chamber or a similar chamber having a Mylar window interposed between the center wire and the filter. Using the windowless chamber, we observed a progressive decrease in sample counting rates. This decrease in the counting rate was avoided by counting the sample for 1 minute, removing it from the chamber, and counting it again at least one-half hour later. This decrease was apparently due to electrostatic charging of the nonconducting filter pads and was a troublesome problem in the dry atmosphere of California. Similar difficulties in counting samples on membrane filters in a windowless chamber were reported by Setter, Hagee, and Straub (1958). The Mylar window completely prevented this charge effect, and reduced the count of a standard C^{14} source by only one-half.

The determinations of algal activity were corrected to zero-thickness by means of empirical algal self-absorption curves. Different volumes of suspensions of radioactive *Dunaliella* cells were filtered to obtain varying thicknesses of algae. These samples were then counted, and the specific activity plotted against thickness (fig. 2). With

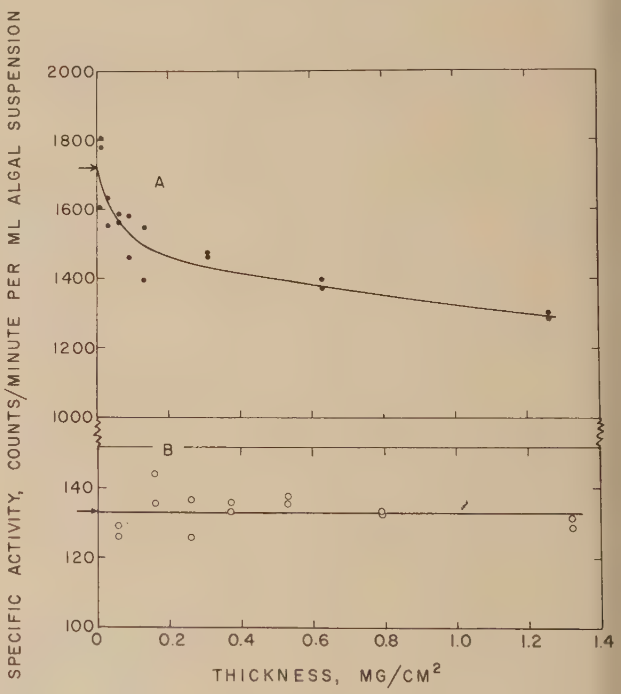

FIGURE 2.—Algal self-absorption curves: (A) Samples counted with a windowless flow chamber; (B) samples counted with a chamber fitted with a Mylar window of approximately 1 mg./cm.^{2} thickness. Solid lines show the empirical extrapolations to zero-thickness activity.

the windowless chamber (curve A), considerable difficulty was experienced in extrapolating from very thin pads (<0.2 mg./cm.^{2}) to zero thickness, and the estimated error of corrections made from curve A is ±6 percent. With the Mylar window, as is shown in curve B, self-absorption corrections appeared to be unnecessary at thicknesses below 1.3 mg./cm.^{2} The standard deviation of the mean of all values for specific activity was ±3 percent. In the experiments reported below, algal thicknesses were never this large.

The radioactivity used in calculating production by the C^{14} method was the mean value obtained by filtering duplicate light bottles minus the mean value from duplicate darkened bottles. The overall precision of the incubation, filtration, and counting procedure was determined by incubating 10 replicate cultures under uniform conditions of illumination and temperature. The standard error of the mean radioactivity taken up in these bottles was ±7 percent.

Total CO_2 in the experimental C^{14} bottles was measured by the excess acid method of Anderson and Robinson (1946), and the equations and factors given by Harvey (1955). A pH meter having a reproducibility of ±0.02 pH unit was used for this determination. An error of ±0.02 units in measuring the final pH after the addition of standard acid results in an error in the total CO_2 concentration of approximately ±6 percent.

Production was calculated from the following equation:

$$\text{Photosynthesis}=\frac{\text{cpm (light)}-\text{cpm (dark)}}{\text{cpm added}}$$

$$\times 1.06 \times \text{total } CO_2/\text{time}$$

The factor 1.06 corrected for the isotope discrimination effect (Steemann Nielsen, 1952). No corrections were made for the respiration of labeled carbon during the incubation nor for excretion of labeled organic matter.

The total experimental error of the C^{14} method in our hands was estimated by pooling all the various sources of error. This was accomplished by taking the square root of the sum of the squares of each error. For windowless counting, the error in the amount of activity added was ±5 percent; the error for incubation, filtration, and counting of activity taken up in replicate bottles was ±7 percent for both light and dark bottles; the error for algal self-absorption was ±6 percent; and the error in total CO_2 was ±6 percent. The pooled total error was thus ±14 percent. With Mylar window counting, some of these individual errors were decreased and the pooled total error was ±13 percent. The windowless counter was used in experiments 1, 2, 4, and 5; the counting chamber fitted with the Mylar window was used in experiments 3, 6, 7, 8, and 9.

OXYGEN METHODS

Oxygen production was measured by filling 67-ml. bottles with the cell suspension. The initial amount of oxygen was measured in one pair of bottles, another pair was darkened with aluminum foil, and the third pair was illuminated. Light and dark bottles were incubated under the same conditions as the C^{14} bottles for periods not exceeding 6 hours. Dissolved oxygen was measured with the Winkler technique using 0.01 normal sodium thiosulfate for the final titration.

A test of the precision of the technique in our hands was made by filling 22 such bottles, measuring the oxygen content in 6 initial bottles, and incubating 6 dark bottles and 10 light bottles. The determinations and their standard errors were as follows: initial oxygen, 5.35 ± 0.03 ml. O_2/1.; dark bottles, 5.08 ± 0.07 ml. O_2/1.; light bottles, 11.51 ± 0.42 ml. O_2/1. The relative errors of each measurement are small, ±1 percent for the initial and dark bottles and ±4 percent for the light bottles. This test showed the relative experimental errors that might be expected when photosynthesis was intense, i.e., using cultures that were still in the logarithmic period of growth and incubating the bottles at high illuminances. Since the amounts of oxygen produced or consumed varied with the conditions prevailing during each experiment, the mean of duplicate bottles was used to determine production and the experimental error of each measurement was determined from the deviation from this mean.

The production of oxygen was converted to carbon production by use of a photosynthetic quotient (O_2/CO_2) of 1.25 as suggested by Ryther (1956). The problem of choosing a correct quotient has been reviewed by Ryther. Under the conditions of our experiments—cells grown with nitrate as an N-source, cells grown at high illuminances, N-deficient cells, etc.—the correct quotient probably lies within ±12 percent of this value. This error is pooled with the experimental error for each oxygen measurement. Pooling of these errors was done in the same manner as with the C^{14} measurements.

ORGANIC CARBON DETERMINATIONS

In experiments 1 and 2, the method of Kay (1954) was used for determining organic carbon in aliquots of the culture suspension. While the combustion mixture, glassware, and the train were similar to those of Kay, absorption of the resulting CO_2 was carried out in the sidearm of a 125-ml. Erlenmeyer flask containing the $Ba(OH)_2$ absorbing solution. This modification was suggested by George Bien of the Scripps Institution of Oceanography. Our mean recovery of 0.5–2.0 mg. of carbon in the form of glucose, methionine, or tryptophane by this method was 98±8 percent. Similar amounts of algal carbon were measured.

In experiment 3, a much less complex method (Strickland and Parsons, 1960) was used to determine algal carbon. Aliquots of the culture suspension containing 1–2 mg. of carbon were filtered on fiber glass filter papers covered with 40 mg. of $MgCO_3$ powder. The filters were then frozen until the analyses could be done. The filters were placed in 30-ml. beakers, and 1 ml. concentrated phosphoric acid was added, followed by 1 ml. of distilled water. The beakers were heated in a boiling water bath for 30 minutes to remove residual chloride ion, and then were cooled. Two ml. distilled water was added, followed by 10 ml. of a dichromate-sulfuric acid oxidizing reagent. After the beakers were heated for an additional 60 minutes and cooled, the solution was decanted into 1-cm. absorption cells. The optical density was measured at 650 mμ against a distilled water blank which was carried through the whole procedure. This procedure differed slightly from that of Strickland and Parsons; instead of measuring the disappearance of dichromate ion (at 440 mμ), the procedure measured the formation of trivalent chromium ion (at 650 mμ). Furthermore, no final dilution was made; thus, a maximum extinction would be measured.

The method was calibrated by analyzing a set of glucose standards with each set of unknown samples. Recovery of tryptophane was 100 percent, but that of methionine was only 50 percent. Thus, some part of the algal carbon may not be completely determined by this method, but this fraction is believed to be quite small (Strickland and Parsons, 1960). The extinction of the samples was corrected by subtracting a blank value obtained by taking a glass filter with $MgCO_3$ through the whole procedure.

The correspondence between the two methods for measuring organic carbon was tested by comparing values for the mean carbon per cell as measured by each method during the logarithmic phase of growth. In experiment 2, with Kay's method, the mean carbon per cell was 35.8 ±6.7 $\mu\mu$g.C/cell; in experiment 3, with the Strickland and Parsons method, it was 41.2 ±7.9 $\mu\mu$g.C/cell. The difference between these experiments was not statistically significant, and a mean value of 39.0 $\mu\mu$g.C/cell was used in converting cell concentration to organic carbon in experiments in which organic carbon was not measured directly.

ORGANIC NITROGEN DETERMINATIONS

In experiments 3 and 4, algal nitrogen was determined by a micro-Kjeldahl method. The cell sample was digested for four hours with a salicylic acid-sulfuric acid mixture (Ranker, 1927) and a copper sulfate-selenium catalyst. Ammonia in the digest was then distilled into boric acid solution and titrated with 0.01 normal sulfuric acid.

LIGHT MEASUREMENTS

Incident illumination was measured with an International Rectifier Corporation B2M selenium photocell. This cell had a spectral sensitivity of 300 to 760 mμ with a peak at 580 mμ. It was calibrated against a Weston foot-candle meter with the same type of light source (a bank of daylight fluorescent tubes) that was used for illuminating the cultures and photosynthetic bottles.

STATISTICAL METHODS

"Student's" parametric *t* test was used to determine statistically significant differences between means of various measurements (Snedecor, 1956). Where sample numbers were small, the nonparameteric Mann-Whitney *U* test was also used (Siegel, 1956).

RESULTS

COMPARISONS OF C^{14} UPTAKE, O_2 EVOLUTION, AND GROWTH DURING THE LOGARITHMIC GROWTH PHASE

Experiment 1

In an initial experiment, several 1,500-ml. cultures of *Dunaliella* were grown at 21° C. and

550 ft.-c. in sea water enriched with 500 μg.-at. NO_3N/l., 50 μg.-at. PO_4-P/l. and 0.25 p.p.m. Fe (as the citrate, Rodhe, 1948). These cultures were not aerated or shaken. When the cultures were visibly green, aliquots were transferred to sterile 67-ml. bottles for C^{14} and O_2 measurements of photosynthesis. Photosynthesis bottles were incubated under the same conditions as the cells were grown. The remainder of the cell suspension was harvested for organic carbon and other growth measurements. The measurements were repeated on 4 successive days. At the end of this period, the pH had risen from 8.0 to 9.2 and growth had ceased.

Table 1 reports corresponding measurements of photosynthesis and increase in organic carbon during this 4-day period. During the first 3 days, C^{14} uptake agreed with net O_2 evolution within the experimental error. This was not the case on the fourth day when C^{14} uptake was probably limited by a decrease in the amount of free CO_2 in solution. The increase in organic carbon was calculated by dividing the difference in organic carbon by the time between samplings. Thus the increase was measured for a longer experimental period than the photosynthetic measurements. This increase was similar to photosynthesis, but was not exactly equivalent to it.

TABLE 1.—*Comparative photosynthesis and organic carbon measurements of cultures of* Dunaliella primolecta

[Experiment 1]

Days	C^{14} uptake	Net O_2 evolution	Gross O_2 evolution	Increase in organic carbon
	μg.C/l./hour	*μg.C/l./hour*	*μg.C/l./hour*	*μg.C/l./hour*
1	18.1± 2.5	23.4± 9.6	24.0± 9.6	----------
2	158 ±22	182 ±24	212 ±26	----------
				208.0
3	124 ±17	125 ±15	187 ±22	
				47.9
4	36.2± 5.1	72.2± 8.8	107 ±20	

Visual observations of these flask cultures showed that they did not all grow to the same extent, i.e., that they were not exactly parallel cultures. Differences between flasks were probably the result of uneven illumination at subsaturating light intensities. In the next experiment a 40-liter mass culture was used instead of several flasks, so that many samples could be taken for an extended period of time from the same culture, and so that CO_2 limitations could be avoided by stirring and aeration.

Experiment 2

For this experiment, twenty 2-liter cultures, containing sea water enriched as in the previous experiment, were inoculated with *Dunaliella.* After 4 days of growth in the culture room at an illuminance of 550 ft.-c. and a temperature of 21° C., during which the cell concentration increased from 3,000 cells/ml. to 118,000 cells/ml., the cell suspension from all twenty cultures was mixed in a plastic-lined aquarium. The aquarium culture was placed in a water bath thermostated at 26° C. and was illuminated from below at an illuminance of 800 ft.-c. The culture was stirred with a glass stirrer coupled to a motor mounted above the aquarium, and 5 percent CO_2-in-air was supplied to the culture through a fritted glass dispersion tube at approximately 300 ml./min. The aquarium was covered with plate glass to reduce evaporation from the culture and contamination by laboratory dust.

After incubation for 24 hours, growth and photosynthesis measurements were started. Seven such sets of measurements were made during the following 48 hours. Photosynthesis bottles were incubated on the bottom of the aquarium and within the culture itself. During the 48-hour period, the pH of the culture was 7.06 to 7.30 and the total CO_2 concentration was 40.2 to 49.7 mg. CO_2–C/1.

Table 2 gives comparative C^{14} uptake and O_2 evolution measurements for this culture. During the first 29 hours of this experiment O_2 evolution (gross and net) generally agreed with C^{14} uptake within experimental error. At zero time, however, C^{14} uptake was somewhat lower than O_2 production. At 35 hours and 48 hours, both net and gross O_2 production were much less than C^{14} uptake. Photosynthesis was probably so intense that the water in the light bottles became supersaturated with O_2 to such an extent that the

TABLE 2.—*Comparative photosynthesis measurements in a 40-liter mass culture of* Dunaliella primolecta

[Experiment 2]

Time	C^{14} uptake	Net O_2 evolution	Gross O_2 evolution
Hours	*μg.C/1./hour*	*μg.C/1./hour*	*μg.C/1./hour*
0	558± 78	789±100	862±100
5	847±120	1,090±130	1,200±150
10	1,440±200	1,500±190	1,630±210
24	2,160±300	1,820±220	1,980±240
29	2,160±300	1,930±230	2,170±260
35	3,610±510	2,000±240	2,330±280
48	5,200±730	1,820±240	2,220±280

production could not be measured as a change in dissolved O_2.

The growth of this culture was measured by increases in cell concentration, dry weight, and organic carbon, and was plotted on a logarithmic scale (fig. 3). From these data, mean logarithmic growth constants (K_2) for each type of measurement were calculated by averaging K_2 values obtained between each sampling time.

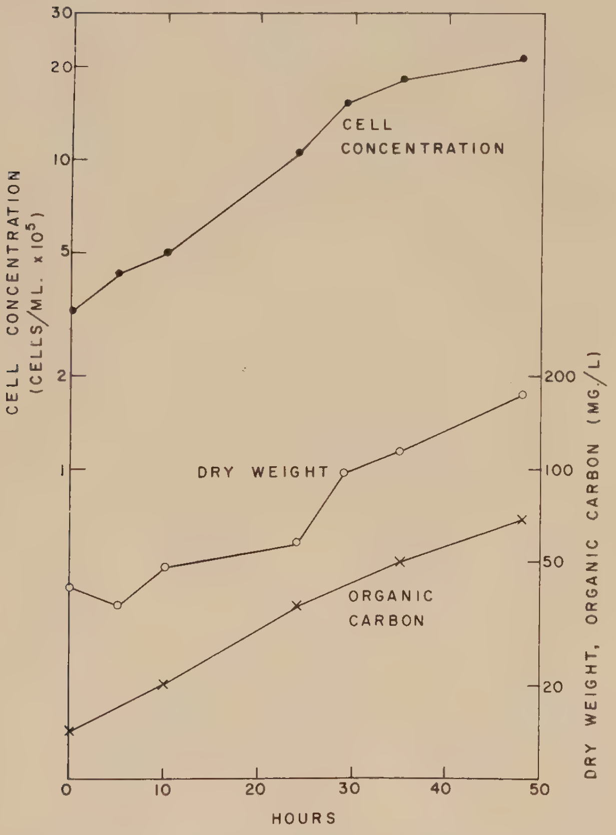

FIGURE 3.—Growth of a mass culture of *Dunaliella primolecta.*

In experiment 1, linear increases in organic carbon were compared with photosynthesis determinations. Obviously, a more meaningful comparison could be made if photosynthesis measurements were converted to logarithmic K_2 values. In the present experiment, the organic carbon measurements provided an initial concentration (C_1) from which photosynthetic K_2 values could be calculated. A sample calculation of a photosynthetic K_2 value is shown in table 3.

TABLE 3.—*Sample calculation of a photosynthetic K_2 value* [1]

$C_1=20.5$ mg.C/1. Photosynthesis (C^{14})$=1.4$ mg.C/1./hour

$$C_2=20.5+1.4=21.9 \text{ mg.C/1.}$$

$$t_1=0$$

$$t_2=1$$

$$K_2=\frac{3.32 \log_{10} 21.9-3.32 \log_{10} 20.5}{1}$$

$$=\frac{3.32\ (1.34044-1.31175)}{1}$$

$$=0.09525 \text{ hours}^{-1}$$

Generation time$=1/0.09525=10.5$ hours

---

[1] Data at 10-hour sampling time, experiment 2.

TABLE 4.—*Mean K_2 values and generation times calculated from growth and photosynthesis measurements in a mass culture of* Dunaliella primolecta

[Experiment 2]

Type of measurement	Mean K_2	Generation time
	Hours^{-1}	*Hours*
Growth:		
Cell concentration	0.0613	16.3
Dry weight	.0492	20.3
Organic carbon concentration	.0470	21.3
Mean of growth values	.0532	18.8
Photosynthesis:		
C^{14} uptake	.0866	11.5
Net O_2 production	.0665	15.0
Mean of photosynthesis values	.0765	13.1

Table 4 gives mean K_2 values and generation times for the three types of growth measurements and two types of photosynthesis measurements in experiment 2. Statistical analysis showed that the K_2 values for the three types of growth measurements did not differ significantly; similarly K_2 values for C^{14} uptake did not differ significantly from those calculated from net O_2 measurements. Also given in table 4 are the overall means for growth and for photosynthesis. This mean growth rate was about 70 percent of the mean photosynthetic rate, and the difference was highly significant ($p<0.01$). Thus, growth in the culture was significantly less than photosynthesis in bottles placed at the bottom of the culture.

Further comparisons of C^{14} uptake, O_2 evolution, and growth were made during the initial logarithmic phases of mass cultures in which growth was eventually limited by nitrogen deficiency (experiments 3 and 4) and by phosphorus deficiency (experiment 6).

EFFECTS OF NITROGEN DEFICIENCY

Experiment 3

This experiment was similar to the previous one, except that the amount of added nitrate was halved, so that growth would be limited by nitrogen deficiency, and the light intensity incident to the bottom of the aquarium culture was increased to alleviate possible light limitations. Two-liter cultures were incubated for 2 days in the culture room at 550 ft.-c. and 21° C. Then they were mixed in the aquarium, supplied with air for 10 hours, and with 5 percent CO_2-in-air thereafter, at a rate of 300 ml./min. Growth and photosynthesis were measured every 10 hours for the next 100 hours and also at 120 hours. Growth was measured by determinations of cell concentration, organic carbon, organic nitrogen, dry weight, and optical density. C^{14} uptake and O_2 evolution were determined as in the previous experiment by placing the photosynthesis bottles in the bottom of the aquarium. At the beginning of these measurements, the pH of the culture was 8.68, at 10 hours it was 6.55, and then increased to a maximum of 7.82 at 120 hours. The total CO_2 concentration was 20.5 mg. CO_2–C/1. at the beginning of the experiment, and thereafter it was 33.1 to 37.9 mg. CO_2–C/1.

Photosynthesis and cell composition measurements are given in table 5; and growth is shown in figure 4. During the first 50 hours, growth in the culture proceeded in a logarithmic fashion and the concentration of nitrogen in the cells was higher than that found in the last three measurements. The C/N ratio was lower. During this period of logarithmic growth, C^{14} uptake agreed well with both net and gross O_2 production.

Mean K_2 values and generation times for the first 50 hours were calculated from the five types of growth measurements (table 6); also reported are the K_2 values and generation times calculated from photosynthesis measurements (C^{14} uptake and net O_2 evolution) and the measured amounts of organic carbon (table 6). The mean growth rate is about 65 percent of the mean K_2 value calculated from photosynthesis measurements. This difference is statistically highly significant ($p<0.01$). As in the previous experiment, growth in the culture was significantly less than photosynthesis in the bottles.

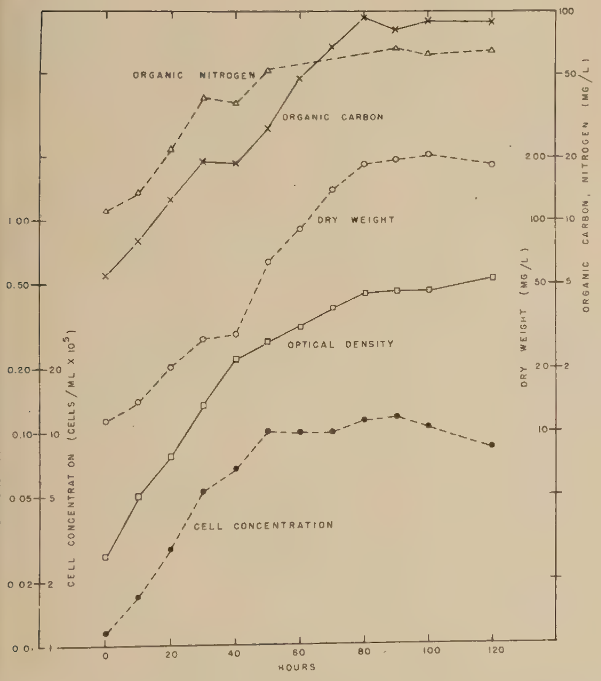

FIGURE 4.—Growth of a mass culture of *Dunaliella primolecta* containing a limiting concentration of nitrogen.

TABLE 5.—*Comparative photosynthesis and cell composition measurements in a mass culture of* Dunaliella primolecta

[Experiment 3]

Time	Photosynthesis			Cell composition	
	C^{14} uptake	Net O_2 evolution	Gross O_2 evolution	*N*	C/N ratio
Hours	µg. C/1./hour	*µg. C/1./hour*	*µg. C/1./hour*	*Percent*	*Atoms*
0	447±58	399±48	447±54	10.00	5.4
10	541±70	564±70	644±80	9.79	6.8
20	772±100	818±100	956±120	10.83	6.8
30	872±110	1,030±130	1,190±140	11.90	5.8
40	1,320±170	1,220±150	1,460±180	9.44	5.9
50	2,830±370	1,870±230	2,380±290	8.20	8.3
60	3,240±420	2,620±330	3,150±390		
70	2,160±280	2,290±270	2,840±340		
80	1,900±250	2,020±240	2,580±320		
90	1,550±200	1,580±190	2,210±260	3.36	14.4
100	1,220±160	1,390±180	1,700±240	3.05	16.8
120	338±44	429±51	880±110	3.64	15.4
123	(2,000 µg.-at./1. N added)				
144	1,350±180	1,200±160	1,670±220	9.48	6.2

TABLE 6.—*Mean K_2 values and generation times during the logarithmic growth phase as calculated from growth and photosynthesis measurements in a mass culture of* Dunaliella primolecta

[Experiment 3]

Type of measurement	Mean K_2	Generation time
Growth:	*Hours⁻¹*	*Hours*
Cell concentration	0.0629	15.9
Dry weight	.0490	20.4
Organic carbon concentration	.0583	17.1
Organic nitrogen concentration	.0430	23.3
Optical density	.0657	15.2
Mean of growth values	.0558	17.9
Photosynthesis:		
C^{14} uptake	.0877	11.4
Net O_2 production	.0841	11.9
Mean of photosynthesis values	.0859	11.6

In the present experiment, optical densities and illuminances at the bottom of the culture were measured. From these measurements, rough calculations could be made of the illuminance at the midheight in the bottles and at midheight in the culture (table 7). The calculations indicate that the culture as a whole received less light than photosynthesis bottles placed on the bottom of the culture. The values given in table 7 refer to measurements made in the center of the aquarium. Although no detailed study was made of the horizontal distribution of light in the aquarium, a few measurements taken near the ends were less than those taken in the center. Thus the culture as a whole may have received even less light than is indicated in table 7.

Table 7.—*Illuminance at the bottom of a mass culture of* Dunaliella primolecta; *illuminance at the midheight of 67-ml. photosynthesis bottles placed on the bottom of the culture; and illuminance at the midheight of the culture itself*

[Experiment 3]

Time	Illuminance		
	At culture bottom	At bottle midheight	At culture midheight
Hours	*Ft.-c.*	*Ft.-c.*	*Ft.-c.*
0	2,070	1,785	1,650
10	1,850	1,500	1,220
20	1,850	1,530	1,280
30	1,750	1,170	720
40	1,620	900	350
50	1,750	880	300
60	1,800	795	310
70	1,850	700	426
80	1,900	610	220
90	1,850	590	200
100	1,850	560	200
120	1,850	495	155

If growth and photosynthesis are proceeding at subsaturating illuminances, the rates of these processes will be dependent upon the light received. Photosynthesis in bottles containing about 10^5 cells per ml. is saturated at an incident illuminance of about 1,200 ft.-c. at 26° C., the temperature of the culture (Thomas, unpublished data). This cell concentration approximates that at zero time in experiment 3. Values close to or less than 1,200 ft.-c. were found in the culture after 10 hours and in the bottles at 30 hours and thereafter (table 7). Thus light probably limited the rate of growth in the culture during most of the initial 50-hour period. At least it seems certain that the culture received less light than the bottles and that this is the reason that K_2 values for growth were less than those for photosynthesis. Probably growth and photosynthesis would have agreed very well if illumination conditions were exactly the same for both types of measurements (see experiment 6).

After 50 hours, cell division ceased in the culture. The amount of nitrogen added to the culture was only half the amount added in the previous experiment, and only about half as many cells were produced. Cells taken at the next three sampling times (60, 70, and 80 hours) were probably in the beginning stages of nitrogen deficiency. Unfortunately, the samples for organic nitrogen taken at these times were lost, but it is unlikely that the organic nitrogen concentration was greater than that found at 70 hours and thereafter.

During this period of incipient deficiency, organic carbon continued to accumulate and the dry weight also increased (fig. 4). Photosynthesis reached a maximum at 60 hours and decreased thereafter (table 5). At 60 hours both gross and net O_2 evolution were less than C^{14} uptake, probably because of supersaturation of the water in the O_2 bottles. At 70 and 80 hours, C^{14} uptake agreed most closely with net O_2 production. During this 60- to 90-hour period, K_2 values for growth, as calculated from organic carbon, optical density, and dry-weight measurements, did not differ significantly from K_2 values calculated from C^{14} uptake and net O_2 production and the measured organic carbon concentration. The mean K_2 value for the growth measurements was 0.0123 hours^{-1} (generation time=24.6 hours), while that for the photosynthesis measurements was 0.0196 hours^{-1} (generation time=15.4 hours).

At 90 hours and thereafter, the effects of nitrogen deficiency were quite marked. The nitrogen in the cells was only 3 to 3.5 percent of the dry weight, the C/N ratio was high, and growth had ceased in the culture (table 5 and figure 4). Photosynthesis continued to decrease and C^{14} uptake agreed well with net O_2 evolution. At 120 hours net O_2 evolution was only half of the gross O_2 evolution, and C^{14} uptake was close to the net O_2 value.

At 123 hours, the culture was brought up to a volume of 28 l. and KNO_3 was added to bring the N concentration to 2,000 μg.-at./1. At 144 hours, growth and photosynthesis measurements were made. During this 21-hour period of recovery from N deficiency, the cell nitrogen increased and and the C/N ratio decreased (see table 5). The culture took up nitrogen at a high rate; the K_2 value for increase in organic N was 0.0926 hours^{-1}.

The cell concentration did not increase, but K_2 values for increases in organic carbon, dry weight, and optical density were 0.0303 hours^{-1}, 0.0268 hours^{-1}, and 0.0122 hours^{-1}, respectively. All photosynthesis values were over twice the amounts recorded at 120 hours, even though the culture had been diluted. Net O_2 evolution was 72 percent of gross O_2 evolution. C^{14} uptake was intermediate between net and gross O_2 evolution. K_2 values calculated from organic carbon concentration at 144 hours and photosynthesis measurements at that time were 0.0329 hours^{-1} (C^{14} uptake) and 0.0294 hours^{-1} (net O_2 evolution).

Experiment 4

In a further investigation of the effects of nitrogen deficiency on photosynthesis, two 20-liter bottles, each containing 6 liters of sea water medium, were inoculated with *Dunaliella.* One bottle was enriched with 2,000 μg.-at.N/1., 200 μg.-at. P/1. and 0.5 p.p.m.Fe, and served as a control culture for comparison with the other bottle, which contained sea water enriched with the same amount of P and Fe, but an amount of N (250 μg.-at./1.) that would limit the final population. Also efforts were made to keep the cultures bacteria-free and to keep the volume of medium in the bottles more constant than in previous experiments. Each bottle was fitted with an air inlet tube extending below the surface of the culture, through which 5 percent Co_2-in-air was supplied at 500 ml./min. The gas was filtered through cotton wool to avoid bacterial contamination. Each bottle was also fitted with a tube for adding fresh sterile medium after each sampling, and with a siphon tube for taking the sample. A final tube was added for the egress of air.

After inoculation, the bottles were placed side by side on a reciprocating shaker which agitated them gently throughout the experiment. The cultures were continuously illuminance from below at an incident illumination of 1,500 ft.-c, and they were incubated at 22° C. in an air-conditioned room. In the control culture (+N), the pH was 6.30 to 6.95, and the total CO_2 concentration was 43.9 to 59.9 mg.CO_2-C/1. In the deficient culture, the pH was 6.28 to 6.69 and the total CO_2 concentration was 39.5 to 51.1 mg.CO_2-C/1.

Samples were taken for growth and photosynthesis measurements at intervals over a period of 8 days. Growth was measured only by cell counts and is expressed in K_2 units and generation times as previously described. Samples for cell nitrogen analyses were centrifuged at 4,400 g. for 20 minutes. The cells were resuspended in distilled water and recentrifuged; they were then transferred to tared glass cups and dried in vacuo at 50° C. Measurement of growth by dry-weight determinations was attempted from these samples, but unavoidable losses of cell material occurred during centrifugation and resuspension. Thus, these samples could only be used to determine the percent N in the cells. After each sample was taken from the cultures, equivalent volumes of fresh media were added, but no nitrogen was added to the N-deficient culture until after 138 hours of incubation.

Photosynthesis bottles were incubated separately from the cultures at 1,250 ft.-c. illuminance and 22° C. These measurements were carried out with portions of the undiluted culture during the first seven samplings; 10-ml. aliquots were diluted with sterile sea water for the last three measurments. Thus, in these latter determinations, light limitations due to mutual shading of the cells were avoided, as were errors due to supersaturation of the suspension with oxygen.

The results of this experiment are given in tables 8 and 9. To compare data from different sampling times, photosynthesis is expressed as the photosynthetic capacity or photosynthesis per cell, as well as in terms of photosynthesis per liter. The condition of the cells in relation to nitrogen is shown by the figures for percent nitrogen in the cells. These nitrogen values are less than those reported in the previous experiment for cells in the same condition. Probably some N was lost during the washing procedure.

During the first 42 hours, mean growth constants, generation times, and photosynthetic capacities were similar in both cultures, but there was considerable variation in these values from sampling time to sampling time in each culture. Mean photosynthesis per cell, from all determinations in both cultures was 2.10 $\mu\mu$ g.C/cell/hour, for C^{14} uptake; 2.02 $\mu\mu$ g.C/hour, for net O_2 production; and 2.88 $\mu\mu$ g.C/cell/hour, for gross O_2 production.

The mean growth constant (K_2) of the −N culture was 0.1058 hours $^{-1}$ (9.5 hours generation time) and 0.1354 hours $^{-1}$ (7.4 hours generation time) in the +N culture. These mean K_2 values

Table 8.—*Growth and comparative photosynthesis measurements of* Dunaliella primolecta *cells containing sufficient nitrogen*

[Experiment 4]

Time, (hours)	Growth		Photosynthesis			Photosynthetic capacity			Nitrogen
	Growth constant between samples K_2 (hours^{-1})	Generation time (hours)	C^{14} uptake µg. C/l./hr.	Net O_2 production µg. C/l./hr.	Gross O_2 production µg. C/l./hr.	C^{14} uptake µµg. C/cell/hr.	Net O_2 production µµg. C/cell/hr.	Gross O_2 production µµg. C/cell/hr.	Cell nitrogen percent of dry weight
0			347±49	342±61	622±90	2.99	2.95	5.36	6.50
	0.1281	7.8							
8			565±79	----------	----------	2.90	------	----	8.15
	.1203	8.3							
24			1,400±200	1,480±190	1,730±220	2.48	2.61	3.04	9.47
	.0912	11.0							
32			991±140	1,570±220	2,620±310	1.24	1.97	3.28	11.13
	.2021	4.9							
42			1,900±270	2,950±440	3,120±270	1.38	2.15	2.27	9.23
	.0411	24.3							
66			2,620±370	2,980±390	3,400±490	1.05	1.19	1.36	----
	.0423	23.6							
90			2,410±340	2,770±360	3,510±460	0.82	0.94	1.19	6.12
	.0443	22.6							
114			918±130	931±150	980±150	1.34	1.35	1.43	8.87
	−.0053	−188.0							
138			697±98	727±90	779±97	1.28	1.34	1.43	8.55
	−.0031	−328.0							
163			583±82	686±96	774±100	1.31	1.44	1.62	6.78

Table 9.—*Growth and comparative photosynthesis measurements in nitrogen-deficient cells of* Dunaliella primolecta

[Experiment 4]

Time, (hours)	Growth		Photosynthesis			Photosynthetic capacity			Nitrogen
	Growth constant between samples K_2 (hours^{-1})	Generation time (hours)	C^{14} uptake µg. C/l./hr.	Net O_2 production µg. C/l./hr.	Gross O_2 production µg. C/l./hr.	C^{14} uptake µµg. C/cell/hr.	Net O_2 production µµg. C/cell/hr.	Gross O_2 production µµg. C/cell/hr.	Cell nitrogen percent of dry weight
0			429±60	333±80	554±99	2.12	1.64	2.74	7.75
	0.0716	14.0							
8			404±57	601±87	767±110	1.62	2.40	3.07	8.77
	.1330	7.5							
24			2,410±340	1,740±220	2,080±260	2.84	2.05	2.45	9.47
	.1247	8.0							
32			3,390±480	2,530±320	3,810±460	2.34	1.75	2.63	3.86
	.0937	10.7							
42			1,210±170	797±110	1,190±160	1.06	0.69	1.04	----
	.0307	32.6							
66			383±54	472±74	891±130	0.21	0.27	0.51	1.77
	.0077	130.4							
90			138±19	171±21	353±42	0.12	0.13	0.28	1.79
	−.0107	−93.3							
114			40.4±5.6	−16.4±.57	8.2±8.5	0.28	−0.11	0.06	2.22
	−.0317	−31.6							
138[1]			6.3±0.9	−7.9±3.6	15.9±2.2	0.08	−0.11	0.21	1.65
	−.0249	−40.2							
163			69.3±9.7	66.3±10.3	91±11	1.66	1.59	2.18	6.86

[1] 2,000 µg. at. N/l added after samples were taken.

did not differ statistically. Photosynthesis bottles were incubated at an illuminance of 1,250 ft.-c., whereas the cultures were incubated at 1,500 ft.-c. Thus, K_2 values calculated from photosyntheesis and organic carbon estimations would not be exactly comparable. However, such K_2 values were calculated. In these calculations, the initial organic carbon (C_1) was estimated by multiplying the mean value for carbon per cell (obtained from the logarithmic phases of experiments 2 and 3) by the cell concentration, and C^{14} uptake or net O_2 evolution values were added to the initial organic carbon estimate to obtain C_2. For cells from the −N culture, the mean of such photosynthetic K_2 values were 0.0800 hours $^{-1}$ (C^{14}) and 0.0706 hours $^{-1}$ (net O_2); respective generation times were 12.5 and 14.1 hours. Cells from the +N culture gave mean K_2 values of 0.0872 hours $^{-1}$ (C^{14}) and 0.0897 hours^{-1} (net O_2), and the generation times were 11.5 and 11.1 hours, respectively. These mean values did not differ statistically. The mean growth constant for both cultures was 0.1200 hours^{-1}; the mean photosynthetic K_2 value calculated from all photosynthesis measurements and organic carbon estimates in both cultures was 0.0810 hours^{-1}. The growth rate was 48 percent greater than the photosynthetic rate and this difference was statistically significant. This difference may be attributed to different illuminances in the culture and in the photosynthesis bottles.

In the control (+N) culture, after 42 hours, photosynthetic capacities were somewhat reduced. C^{14} uptake agreed most closely with net O_2 production, but neither C^{14} nor net O_2 production differed from gross O_2 production by an amount greater than the experimental error of the measurements. Although the growth rate decreased and growth eventually ceased, photosynthesis and photosynthetic capacity were not strongly inhibited. The reduction in growth rates and in photosythetic capacities was probably due to light limitations in the very dense culture. The culture retained its bright green appearance, and the concentration of N in the cells did not change greatly.

After 42 hours, N deficiency was very marked in the −N culture, which was pale green in color. Much less nitrogen was found in the cells. During the next 48 hours, growth continued at a reduced rate and the photosynthetic capacity was greatly reduced. Net oxygen production fell from the usual 70 to 90 percent of gross production to 50 percent of gross production. C^{14} uptake agreed with net production during this period. N-deficient cells stained more heavily with Lugol's dine solution and more of them were nonmotile ian cells in the +N culture.

After 90 hours, growth constants were negative the −N culture. Net photosynthesis was egative, and C^{14} uptake agreed more closely with ross O_2 evolution.

After 138 hours, 2,000 µg.-at.N/1. were added the—N culture. Although the cell concentra- on did not increase during the next 23 hours, the notosynthetic capacity increased greatly. C^{14} ptake agreed closely with net O_2 production. o measurements were made beyond this point, ut the culture was very much more green and ense on the following day.

In this experiment on nitrogen deficiency, septic technique was employed to keep the ilture bottles bacteria-free. This point was hecked at each sampling time by adding a portion the sample to a tube of sea water enriched with percent dextrose and 5 percent peptone. These ibes became turbid with bacterial growth in 3 ays at room temperature. Thus, bacteria were ndoubtedly present, although contamination as probably not great, since turbidity did not evelop in less than 3 days.

xperiment 5

To study the effects of N deficiency on photo- ynthesis in the absence of bacteria, small-scale, acteria-free cultures containing limiting and ifficient amounts of nitrogen were inoculated ith *Dunaliella*. One-liter Erlenmeyer flasks con- iining 700 ml. of the same +N and −N media sed in experiment 4 were incubated on the eciprocating shaker at 1,000 ft.-c. illuminance nd 22° C. No aeration was provided, and after days the pH had risen from 8.1 to 9.2 in both iltures, and growth had ceased. Then 15 mil- moles of sodium bicarbonate were added asep- cally to each culture. After 3 more days, ie pH had risen again to 9.1. The −N culture as pale green, while the +N culture was bright reen in appearance. For photosynthesis meas- rements, 10-ml. portions of each culture were ien added to 50 ml. sterile sea water containing 2 ml. 0.5 molar $NaHCO_3$ in 67-ml. bottles. ottles for O_2 measurements were filled with erile sea water, and C^{14} bottles received 1 ml. C^{14} solution. The pH in these bottles was 6. The bottles were incubated on the shaker nder the same conditions of illuminance and mperature that were used to grow the cells. Peptone-dextrose sterility test tubes showed that bacteria were absent from these cultures. The results of these photosynthesis measurements are shown in table 10.

TABLE 10.—*Photosynthesis in* N-*deficient and* N-*sufficient bacteria-free cultures of* Dunaliella primolecta

[Experiment 5]

Measurements	Culture	
	−N	+N
Photosynthesis:		
C^{14} uptake (µg.C/1./hour)	300±42	834±120
Net O_2 production (µg.C/1./hour)	309±37	933±110
Gross O_2 production (µg.C/1./hour)	380±46	1,010±120
Photosynthetic capacity:		
C^{14} uptake (µµg.C/cell/hour)	1.33	2.77
Net O_2 production (µµg.C/cell/hour)	1.37	3.09
Gross O_2 production (µµg.C/cell/hour)	1.68	3.35

The ratio of net O_2 evolution to gross O_2 evolution in the N-deficient culture was 81 percent, while that in the control (+N) culture was 91 percent. Thus the effects of deficiency were not as pronounced as those shown by measurements taken after 40 hours in the previous experiment. In both cultures, C^{14} uptake agreed most closely with net O_2 production.

EFFECTS OF PHOSPHORUS DEFICIENCY

Experiment 6

To study the effects of phosphorus deficiency on photosynthesis and growth, the mass culture apparatus (aquarium) was again used. Forty liters of sterilized sea water were placed in the aquarium and enriched with 2,000 µg.-at. N/1., 1 p.p.m. Fe, and a limiting concentration of P (20 µg.-at./1.). The culture was inoculated with *Dunaliella* and incubated for 19 hours before growth and photosynthesis measurements were begun. During this period no CO_2 was supplied, but the culture was stirred with a glass stirrer. The aquarium was incubated at 26° C. and continuously illuminated from below at an illuminance of 800 ft.-c.

After the 19-hour preliminary period, 5 percent CO_2-in-air was supplied at 300 ml./min. for the rest of the experiment. Temperature, illumination, and stirring conditions were maintained at the level previously set. When the initial sample was taken, the pH of the culture was 8.05 and varied from 6.22 to 6.89 thereafter. Similarly, the initial CO_2 concentration was 23.0 mg. CO_2–C/1. and varied from 33.7 to 44.6 mg. CO_2–C/1. for the rest of the experiment. Growth was measured by cell concentration and by optical density measurements. Photosynthesis was measured as previously described by placing the bottles on the bottom of the culture.

The growth of the culture is depicted in figure 5 and photosynthesis measurements are given in table 11. The initial cell concentration and optical density were too low to measure. Initial photosynthesis rates were correspondingly low; C^{14} uptake agreed with net O_2 evolution within the experimental error at this low phytoplankton concentration.

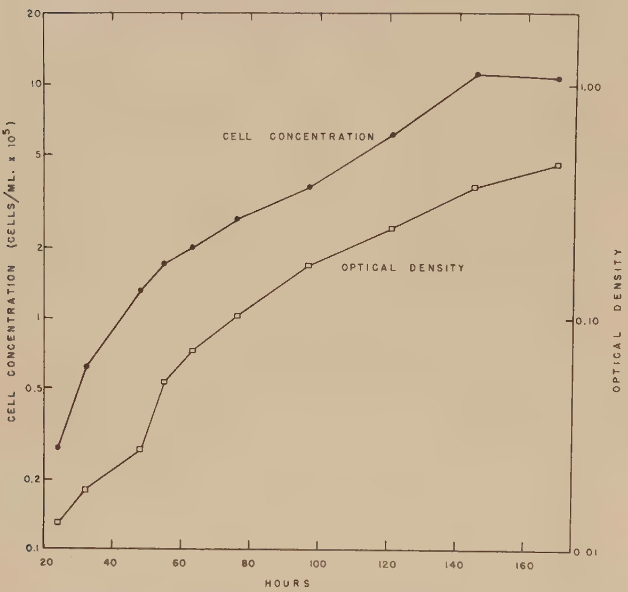

FIGURE 5.—Growth of a mass culture of *Dunaliella primolecta* containing a limiting concentration of phosphorus.

TABLE 11.—*Comparative photosynthetic measurements at 800 ft.-c. during the development of phosphorus deficiency in a mass culture of* Dunaliella primolecta

[Experiment 6]

Time (hours)	Photosynthesis			Photosynthetic capacity		
	C^{14} uptake μg.C/1./hour	Net O_2 production μg.C/1./hour	Gross O_2 production μg.C/1./hour	C^{14} uptake $\mu\mu$g.C/cell/hour	Net O_2 production $\mu\mu$g.C/cell/hour	Gross O_2 production $\mu\mu$g.C/cell/hour
0	11±1	19±8	---------	---------	---------	---------
24	112±15	135±27	154±20	4.06	4.88	5.58
32	126±16	157±20	188±24	2.07	2.56	3.06
48	231±30	279±36	423±51	1.77	2.13	3.24
55	371±48	367±60	449±67	2.18	2.16	2.64
63	475±62	541±70	678±82	2.41	2.73	3.42
76	764±99	667±110	864±130	2.88	2.50	3.24
97	1,350±180	1,060±160	1,210±180	3.69	2.88	3.31
121	1,580±210	1,470±160	1,640±200	2.58	2.41	2.67
145	1,320±170	1,090±150	1,740±230	1.19	0.98	1.56

During the period from 24 to 55 hours, rapid logarithmic growth occurred in the culture. C^{1} uptake agreed most closely with net O_2 production The mean growth rates (K_2) were 0.0884 hours^{-1} and 0.0781 hours^{-1}, as determined by cell concentrations and optical density measurements respectively. Cell concentrations were converted to an estimated organic carbon concentration which was used in calculating photosynthetic K_2 values from C^{14} uptake and net O_2 production measurements. These mean photosynthetic K_2 values were 0.0843 hours^{-1} and 0.1048 hours^{-1} as calculated from C^{14} uptake and net O_2 production respectively. The overall mean K_2 for growth was 0.0835 hours^{-1}, while that for photosynthesis was 0.0945 hours^{-1}. Statistical tests showed that these mean K_2 values did not differ significantly Rough calculations of illuminances in the bottles and at midheight in the culture showed that at 24, 32, and 48 hours these illuminances did not differ by more than 10 percent, and at 55 hours illuminance in the bottles was 25 percent greater than illuminance at the midheight of the culture Thus during this period before the culture became too dense, illumination conditions were nearly equivalent in the culture and in photosynthesis bottles placed on the bottom of the culture, and photosynthesis was equivalent to growth.

The growth rate of the culture was much reduced during the period from 55 to 145 hours. The mean growth constant K_2, as calculated from increases in cell concentration, was 0.0291 hours^{-1} that calculated from increases in optical density was 0.0344 hours^{-1}. K_2 values calculated from photosynthesis determinations and estimated organic carbon concentrations were 0.0892 hours^{-} (C^{14}) and 0.0761 hours^{-1} (net O_2). The overall mean photosynthetic constant was 0.0827 hours^{-1} that for growth was 0.0317 hours^{-1}. Statistical tests showed that this difference was significant Growth in the culture proceeded at only about 40 percent of the rate of photosynthesis in bottles placed on the bottom of the culture. Rough calculations of light intensities showed that the intensity at midheight in the culture was only 45–75 percent of that in the bottles.

During this 90-hour period, C^{14} uptake corresponded to both net or gross O_2 evolution, which did not differ greatly from each other. Further indications that light was limiting in the culture were found by incubating a duplicate set of photo ynthesis bottles at 1,800 ft.-c. These photo-ynthesis measurements are shown in table 12. Photosynthetic capacities were greatly increased y incubation at this light intensity, and C^{14} up-ake was similar to both net and gross O_2 roduction.

ABLE 12.—*Comparative photosynthesis determinations at 1,800 ft.-c. during the development of phosphorus deficiency in* Dunaliella primolecta

[Experiment 6]

Time (hours)	Photosynthesis			Photosynthetic capacity		
	C^{14} uptake µg.C/1./hour	Net O_2 production µg.C/1./hour	Gross O_2 production µg.C/1./hour	C^{14} uptake µµg.C/cell/hour	Net O_2 production µµgC/cell/hour	Gross O_2 production µµg.C/cell/hour
6	1,440±190	1,170±140	1,370±170	5.44	4.39	5.13
97	2,010±260	1,810±220	1,970±240	5.48	4.93	5.36
21	2,330±300	2,360±290	2,520±310	3.82	3.85	4.12
45	2,310±300	1,880±230	2,520±310	2.08	1.68	2.26

At 145 hours, cell division ceased, but optical ensity continued to increase for an additional 24 ours. To test for phosphorus deficiency, 50-ml. liquots of the cell suspension were placed in four 25-ml. flasks at 153 hours. Two flasks were en-iched with phosphorus at a concentration of 20 g.-at.P/1. Two others received no addition. he flasks were incubated for 16 hours at 1,500 t.-c and 22° C. on a reciprocal shaker. The initial ptical density was 0.409; after 24 hours the optical ensity of cultures to which phosphate was added as 0.561, while that of the control (—P) cultures as 0.481. Thus, the increase in optical density as greater in cultures which contained added hosphate than in control cultures. The cells ere undoubtedly phosphorus-deficient, but only the beginning stages of deficiency, since some rowth (increase in optical density) occurred in he culture and in the flasks to which no phos-horus was added. At 145 hours, for bottles laced in the culture and incubated at an incident luminance of 800 ft.-c, net O_2 production was 62 ercent of the gross value. These net gross ratios re generally less than those found earlier in this xperiment, and are also indicative of the begin-ing stages of phosphorus deficiency. At 145 ours, C^{14} uptake was intermediate between, but id not differ significantly from, net and gross O_2 volution. Photosynthesis was not measured at 69 hours.

Experiment 7

Another experiment on the effects of phosphorus deficiency was performed with small-scale, bacteria-free cultures containing limiting and sufficient amounts of phosphate. One-liter Erlenmeyer flasks containing 700 ml. of media were inoculated with *Dunaliella* and incubated on the reciprocal shaker at 1,600 ft.-c. and 26° C. The complete (+P) medium consisted of sea water enriched with 2,000 µg.-at. NO_3-N/1.,200 µg.-at. PO_4-P/1. and 1 p.p.m. Fe. In the phosphorus-deficient culture the sea water was enriched with only 20 µg.-at. PO_4-P/1.

After 188 hours, the —P culture contained 7,700-000 cells/ml., while the +P culture contained 9,500,000 cells/ml. Sixty-seven-ml. bottles containing 50 ml. sea water and 0.1 millimole of $NaHCO_3$ were inoculated with 10-ml. portions of each culture. Bottles for O_2 measurements were then filled with sterile sea water, those for C^{14} measurements received 1 ml. C^{14} solution. They were incubated at 1,400 ft.-c. and 25° C.

Table 13 shows the results of this experiment with bacteria-free cultures. In the control (+P) culture, C^{14} uptake agreed quite well with net O_2 production. In the phosphorus deficient culture, it was much less than either net O_2 production or gross O_2 production.

TABLE 13.—*Photosynthesis in P-deficient and P-sufficient bacteria-free, cultures of* Dunaliella primolecta

[Experiment 7]

Measurements	—P Culture	+P Culture
Photosynthesis:		
C^{14} uptake (µg.C/l./hour)	165±21	511±66
Net O_2 production (µg.C/l/hour)	272±33	504±61
Gross O; production (µg.C/l./hour)	318±39	542±66
Photosynthetic Capacity:		
C^{14} uptake (µµg.C/cell/hour)	1.07	2.69
Net O_2 production (µµg.C/cell/hour)	1.77	2.65
Gross O_2 production (µµg.C/cell/hour)	2.06	2.85

COMPARATIVE MEASUREMENTS OF PHOTOSYNTHESIS BY pH CHANGES, C^{14} UPTAKE, AND O_2 EVOLUTION

Experiments 8 and 9

In previous experiments, C^{14} uptake was compared with O_2 evolution and with growth. It appeared desirable to compare C^{14} uptake with measurements of CO_2 assimilation that were more direct than determinations of O_2 evolution and growth. By using cultures where the rate of photosynthesis was high (cultures in the logarithmic growth phase, and incubated at high illuminances), it was feasible to measure CO_2

assimilation directly from pH changes and to compare CO_2 assimilation with C^{14} uptake and O_2 evolution.

Cells for these comparisons were grown in sea water enriched with 2,000 µg.-at. NO_3-N/l., 200 µg.-at. PO_4-P/l. and 1 p.p.m. Fe. After 6 days of growth at 500 ft.-c. and 26° C., 25 ml. of the cell suspension was added to 25 ml. of sterile sea water containing 0.1 ml. of 0.5 molar $NaHCO_3$ in 67-ml. bottles. Bottles for O_2 and pH measurements were filled with sterile sea water; those for C^{14} measurements received 1-ml. C^{14} solution. All bottles were incubated at 23° C. and 1,450 ft.-c.

The results of these experiments are shown in table 14. The pH changed in the first experiment from 8.66 to 8.88 during 3¼ hours of incubation; in the second experiment it changed from 8.15 to 8.98 during four hours. From these changes and the carbonate alkalinity, the amount of CO_2 taken up was calculated. The total (pooled) error of the pH method was ±8.5 percent—±6 percent for each measurement, beginning and final. In both experiments CO_2 assimilation as measured by pH changes agreed with that measured by C^{14}. O_2 measurements were also equivalent to both CO_2 measurements within the experimental error.

TABLE 14.—*Photosynthesis in* Dunaliella primolecta *as measured by pH changes, C^{14} uptake, and O_2 evolution*

Type of measurement	Experiment 8	Experiment 9
pH change (µg.C/l./hour)	1,380±120	2,770±240
C^{14} uptake (µg.C/l./hour)	1,720±220	2,670±350
Net O_2 production (µg.C/l./hour)	1,300±160	2,230±260
Gross O_2 production (µg.C/l./hour)		2,350±280

DISCUSSION

Under conditions of adequate nutrition and illuminance, the difference between total or "gross" O_2 evolution and net O_2 evolution is not large. Commonly the difference is only 5–20 percent. To compare such measurements with C^{14} uptake it is necessary to calculate the equivalent carbon production using a photosynthetic quotient (O_2/CO_2) which may vary nearly as much (±12 percent, Ryther, 1956) as the experimental error of the C^{14} method. The present results show that, under these ideal conditions, C^{14} uptake agrees well with net O_2 evolution, but does not differ greatly (and often not significantly) from gross O_2 evolution either. This was shown by experiments using cells taken from the logarithmic phases of growth in the aquarium cultures (experiments 1, 2, 3, and 6) and in control cultures (+N and +P) of the experiments on N and P deficiency (experiments 4, 5, and 7). These results agreed with those of other investigators who have used healthy cultures to compare O_2 evolution and C^{14} uptake (Ryther, 1954; Ryther and Vaccaro, 1954; Steemann Nielsen and Al Kholy, 1956; Ichimura and Saijo, 1958).

The growth of an algal culture is also a net process, and such growth is more representative of an increase in the food which would be available to zooplankton, for instance, than is net O_2 evolution. In the present experiments, growth was measured in several ways and logarithmic growth constants were calculated from these growth measurements. Organic carbon determinations provided a way of converting photosynthesis measurements to similar K_2 values, so that photosynthesis could be compared with growth.

In experiments 2 and 3, growth was somewhat less than photosynthesis as measured by C^{14} uptake and net O_2 evolution. This difference was attributed to differences in the illumination of cells in photosynthesis bottles placed within the culture and that reaching the culture itself. At low cell densities (experiment 6), when illuminance in the bottles was similar to that in the culture, growth and photosynthesis did not differ. In experiment 4, when the illuminance in the culture was greater than that in the bottles, growth was greater than photosynthesis. These results indicate that during the logarithmic phase of growth, if conditions are the same for the two measurements, growth and photosynthesis are similar, and that C^{14} measurements are equivalent to increase in algal biomass. It would have been more desirable to compare C^{14} uptake and growth in the same vessel, but a frequent sampling routine could not have been maintained. Furthermore, glass-stoppered bottles are used as containers for photosynthesizing cells in field C^{14} measurements, and it was desired to approximate field conditions as much as possible.

Using a natural phytoplankton population enclosed in a large plastic bag, McAllister et al. (1961) have recently compared several methods of measuring production. During the logarithmic phase of growth in the bag, measurements nade with the C^{14} method were approximately quivalent to those calculated from O_2 changes, H changes, increases in organic carbon, and ncreases in cell volume (see their fig. 7). This quivalence between growth and photosynthesis vas confirmed by our results with *Dunaliella* ultures.

In the sea, rapid logarithmic phytoplankton rowth is probably not common. It occurs nainly during the spring outburst in temperate vaters, and during the development of "red ides." In most tropical and subtropical seas, t least, incipient nutrient deficiency is probably more common condition, a condition under vhich phytoplankton grow and produce organic natter at a rate which is limited by the rates of uch processes as the remineralization of nutrients n the surface layers or slow diffusion from ubsurface supplies.

Incipient nitrogen deficiency in *Dunaliella* was tudied in experiments 3 and 4. Under such onditions, C^{14} uptake was similar to net O_2 volution. During the period of incipient de- ciency, K_2 values for increases in organic carbon alculated from photosynthesis measurements did ot differ significantly from those calculated for rowth.

It is also interesting to note that incipient itrogen deficiency resulted in a change in netabolism—a "shunt" in which cell material is ormed which is low in nitrogen. During loga- thmic growth, some 8 to 10 percent of the dry eight was nitrogen. During incipient deficiency, itrogen made up only 3 percent of the dry eight and carbon continued to accumulate. hus, the C/N ratio shifted from approximately x during the logarithmic growth period to pproximately 15 when the cells became deficient see table 5). The main product of this shunt netabolism was probably starch, since deficient ells were stained more heavily by iodine. Similar hifts in metabolism from predominantly protein ormation to carbohydrate or lipid formation ave been reported for other green algae when itrogen was deficient (Spoehr and Milner, 949; and others).

Extreme nutrient deficiency is probably of nore academic than oceanographic significance. Vhen deficiency becomes extreme, net O_2 produc- ion falls below 50 percent of gross O_2 production. teemann Nielsen and Al Kholy (1956) pointed out that a phytoplankton population would not persist in nature under such conditions. During the night, respiration would presumably continue at the same rate as during the day, and, assuming a 12-hour day-length, gross photosynthesis must be at least twice the amount of respiration. This point was reiterated by Strickland (1960). Extreme nitrogen deficiency was achieved in one of the present experiments (experiment 4); C^{14} uptake agreed most closely with gross O_2 production under this condition. At this time, the photosynthetic capacity was much reduced; and growth constants and net O_2 evolution were negative.

Ryther (1954), using a related alga, *D. euchlora*, presented data on the effects of nutrient deficiency on C^{14} and O_2 measurements. He gave no details about the culture conditions used in growing the alga, so that one cannot tell whether his results were due to nitrogen or to phosphorus deficiency. After 15 days of growth, however, net O_2 production was 50 percent of gross O_2 production; after 30 days, net production was only about 5 percent of gross production. In both cases, C^{14} uptake agreed well with net O_2 production. On the other hand, Steemann Nielsen and Al Kholy (1956), using the fresh-water green alga, *Chlorella pyrenoidosa*, showed that C^{14} uptake in nitrogen- and phosphorus-deficient cultures did not differ greatly from gross O_2 production. The conditions of their cultures appear to approach those of Ryther after 30 days of growth, since net O_2 production was only a small fraction of gross O_2 production.

Results given in experiments 3 and 4 indicate that C^{14} uptake agrees closely with net O_2 production during a period of incipient nitrogen deficiency. These data agree with those obtained by Ryther in 15-day cultures. Furthermore, the agreement between growth and photosynthesis under these conditions also suggests that the C^{14} method measures a net increase in algal biomass.

The effects of extreme nitrogen deficiency were less clear. In the latter stages of experiment 4, when the cells were extremely deficient, net O_2 evolution was negative, and C^{14} uptake corresponded more closely with gross O_2 production. This result is more in agreement with the comparisons of Steemann Nielsen and Al Kholy than those of Ryther. However, the low values for net O_2 evolution in experiment 4 may be erroneous due to bacterial contamination. Cells from an older, bacteria-free culture (experiment 5), which may also have been extremely nitrogen-deficient, assimilated C^{14} at a rate which corresponded to net O_2 evolution. Obviously, further studies of the effects of extreme nitrogen deficiency in bacteria-free culture would be of interest but would be less significant than investigations of incipient deficiency.

Phosphorus deficiency was not studied in as great detail as nitrogen deficiency. In the latter stage of experiment 6 (tables 11 and 12), with cells that were probably in a stage of incipient deficiency, C^{14} uptake did not differ significantly from either net or gross O_2 production, and was intermediate between the two O_2 values. In another phosphorus-deficient culture (experiment 7), which was also bacteria-free and was older than that of experiment 6, C^{14} uptake was much less than net O_2 evolution. Phosphorus deficiency in this experiment may have been more extreme than in experiment 6, and, under such conditions, soluble, C^{14}-labelled, organic matter might have been excreted by *Dunaliella* cells. Such material would not have been collected on the membrane filter and included in the measurement of C^{14} uptake.

In another test of the general validity of the C^{14} method, C^{14} uptake was shown to be equivalent to the uptake of CO_2 as measured by pH changes. These experiments (8 and 9) were carried out with healthy cells.

To relate studies with laboratory cultures to C^{14} measurements carried out in the open sea, it would be necessary to use cultures of representative oceanic phytoplankton species in experiments such as these. *D. primolecta* may only be representative of the phytoplankton of British coastal waters, from which it was isolated (Butcher, 1959), and caution is necessary in applying the results of the present experiments to measurements of oceanic photosynthesis.

To the extent that *Dunaliella* is a representative alga, however, these experiments indicate that the C^{14} method provides a reliable measure of net photosynthesis and of increase in phytoplankton biomass, under good conditions for phytoplankton growth and under conditions of incipient nitrogen deficiency. Fortunately, cultures of representative oceanic phytoplankton are becoming available (Thomas, 1959), and could be used for further studies of the C^{14} method.

SUMMARY

1. During the logarithmic phase of growth of cultures of *D. primolecta*, photosynthetic C^{14} uptake agreed well with net O_2 production, but also did not differ greatly from gross O_2 production.

2. During this growth phase, the growth rate of mass cultures was generally less than the photosynthetic rate (C^{14} uptake and net O_2 production) in bottles of the cell suspension placed within the culture. This difference was attributed to different illumination conditions between the bottles and the culture. In one experiment, when illumination conditions were similar, growth in the culture was equivalent to photosynthesis in the bottles.

3. In cultures that were incipiently nitrogen-deficient, C^{14} uptake was similar to net O_2 production and growth was equivalent to photosynthesis.

4. In one experiment, under conditions of extreme nitrogen deficiency, C^{14} uptake was greater than net O_2 evolution, and more closely approximated gross O_2 evolution. In another such experiment, C^{14} uptake agreed well with net O_2 evolution.

5. Nitrogen deficiency in *Dunaliella* suppresses the formation of protein and a carbohydrate, probably starch becomes a major component of the cells.

6. In one experiment, C^{14} uptake in an incipiently phosphorus-deficient culture was intermediate between net and gross O_2 evolution; in another experiment, C^{14} uptake was less than net O_2 production in a phosphorus-deficient culture.

7. C^{14} uptake in healthy cultures of *Dunaliella* was equivalent to the uptake of CO_2 as measured by pH changes.

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LITERATURE CITED

nderson, Don H., with Rex J. Robinson.
1946. Rapid electrometric determination of the alkalinity of sea water using a glass electrode. Industrial and Engineering Chemistry (Analytical Edition), vol. 18, No. 12, pp. 767–769.

utcher, R. W.
1959. An introductory account of the smaller algae of British Coastal waters. Part I: Introduction and Chlorophyceae. Ministry of Agriculture, Food, and Fisheries (U.K.), Fisheries Investigations, series IV, pp. 1–74.

oty, Maxwell S., and Mikihiko Oguri.
1958. Selected features of the isotopic carbon primary productivity technique. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Réunions, vol. 144, pp. 47–55.

arvey, H. W.
1955. The chemistry and fertility of sea water. Cambridge University Press, Cambridge, 224 pp.

himura, Shun-ei, and Yatsuka Saijo.
1958. On the application of C^{14} method to measuring organic matter production in the lake. The Botanical Magazine, Tokyo, vol. 71, No. 839, pp. 174–180.

tts, H. R., and B. D. Scott.
1961. The determination of zero-thickness activity in Geiger counting of C^{14} solutions used in marine productivity studies. Limnology and Oceanography, vol. 6, No. 2, pp. 116–123.

ay, Hans.
1954. Eine Mikromethode zur chemischen Bestimmung des organisch gebunden Kohlenstoffe im Meerwasser. Institut für Meereskunde an der Universität Kiel. Kieler Meeresforschungen, Band 10, Heft 1, pp. 26–36.

rauss, Robert W., and William H. Thomas.
1954. The growth and inorganic nutrition of *Scenedesmus obliquus* in mass culture. Plant Physiology, vol. 29, No. 3, pp. 205–214.

cAllister, C. D., T. R. Parsons, K. Stephens, and J. D. H. Strickland.
1961. Measurements of primary production in coastal sea water using a large volume plastic sphere. Limnology and Oceanography, vol. 6, No. 3, pp. 237–258.

Ranker, Emory R.
1927. A modification of the salicylic-thiosulfate method suitable for the determination of total nitrogen in plants, plant solutions, and soil extracts. Journal of the Association of Official Agricultural Chemists, vol. 10, No. 2, pp. 230–251.

Rodhe, Wilhelm.
1948. Environmental requirements of fresh-water plankton algae. Botaniska Institutionerna i Uppsala. Symbolae Botanicae Upsalienses, vol. 10, No. 1, pp. 1–149.

Ryther, John H.
1954. The ratio of photosynthesis to respiration in marine plankton algae and its effect upon the measurement of productivity. Deep-Sea Research, vol. 2, No. 2, pp. 134–139.

Ryther, John H.
1956. The mesaurement of primary production. Limnology and Oceanography, vol. 1, No. 2, pp. 72–84.

Ryther, J. H., and R. F. Vaccaro.
1954. A comparison of the oxygen and C^{14} methods of measuring marine photosynthesis. Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil, vol. 20, No. 1, pp. 25–34.

Setter, L. R., G. R. Hagee, and C. P. Straub.
1958. Analysis of radioactivity in surface waters—practical laboratory methods. American Society for Testing Materials Bulletin No. 227, pp. 35–40.

Siegel, Sidney.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, N.Y., 312 pp.

Snedecor, George W.
1956. Statistical methods. 5th ed. Iowa State College Press, Ames, Iowa, 534 pp.

Spoehr, H. A., and Harold W. Milner.
1949. The chemical composition of Chlorella; effect environmental conditions. Plant Physiology, vol. 24, No. 1, pp. 120–149.

Steemann Nielsen, E. and R. F. Vaccaro.
1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil, vol. 18, No. 2, pp. 117–140.

Steemann Nielsen, E., and A. A. Al Kholy.
1956. Use of C^{14}-technique in measuring photosynthesis of phosphorus or nitrogen deficient algae. Physiologia Plantarum, vol. 9, No. 1, pp. 144–153.

Steinberg, Daniel, and Sidney Udenfriend.
1957. The measurement of radioisotopes. *In* Sidney P. Colowick and Nathan O. Kaplan, eds., Methods in Enzymology, vol. 4, pp. 425–472. Academic Press, New York.

Strickland, J. D. H.
1960. Measuring the production of marine phytoplankton. Fisheries Research Board of Canada Bulletin No. 122, 172 pp.

Strickland, J. D. H., and T. R. Parsons.
1960. A manual of sea water analysis. Fisheries Research Board of Canada Bulletin No. 125, 185 pp.

Sweeney, Beatrice M., and J. Woodland Hastings.

1957. Characteristics of the diurnal rhythm of luminescence in Gonyaulax polyedra. Journal of Cellular and Comparative Physiology, vol. 49, No. 1, pp. 115–128.

Thomas, William H.

1959. The culture of tropical oceanic phytoplankton. *In* International Oceanographic Congress Preprints, Mary Sears, ed., pp. 207–209.

Thomas, William H.

1963. Physiological factors affecting the interpretation of phytoplankton production measurements *In* Maxwell S. Doty, editor, Proceeding of th Conference on Primary Productivity Measurement Marine and Freshwater. U.S. Atomic Energ Commission. TID–7633, Biology and Medicine pp. 147–162.

DENTITION OF THE NORTHERN FUR SEAL

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ABSTRACT

Gross morphology and development of deciduous and permanent teeth of *Callorhinus ursinus* are described. The deciduous teeth are essentially nonfunctional; two-thirds of them are usually shed in fetal life. The permanent teeth begin to calcify very early; all have erupted from the jaw, though not all from the gum, at birth. Root growth continues through life, especially in teeth which retain an open pulp canal for 20 years. The 1st premolar and all molars in each quadrant are primary permanent teeth. A "lower 1st incisor" was presumably lost in the evolution of the seal. Cusplets and a double root on certain teeth suggest that modern teeth are derived from more complex ones. In 11 percent of specimens, supernumerary or prenatally absent teeth are recorded.

Purpose

Since 1867 the U.S. Government has managed the Alaska fur seal herd. The seals breed on the Pribilof Islands, and their population in midsummer is about 1,800,000. To improve the management of the herd, the Government obtains zoological information about the animals in its care. In 1949, in the course of exploratory research, Fish and Wildlife Service biologists found that fur seal teeth have layers which correspond in number to the age of the individual in years (Scheffer, 1950). This finding has proved to be useful, and biologists now engaged in applied research have identified the ages of more than 50,000 seals killed during the past decade.

The study of fur seal dentition has continued so that we could gain a better understanding of variation in the teeth and jaws with age and sex. One purpose of the present paper is to trace the origin, growth, and disappearance of the deciduous (milk) teeth which erupt from the bony alveolus in early fetal life. Another purpose is to trace the origin and growth of the permanent teeth which normally erupt from the bony alveolus in late fetal life.

Previous Research

While the dental formula for the fur seal *Callorhinus ursinus* has been known for nearly a century, the ontogeny of the dentition has not been well described. The young fur seal is extremely precocious, and its dentition is determined and developed in utero during winter and spring when the pregnant female is at sea. Because of prohibitions against killing seals at sea, biologists were unable, until 1950, to obtain fetuses. Between 1958 and 1962 they took annually for research purposes about 900 pregnant females along the oceanic migration routes.

Certain papers have contributed to our understanding of the teeth of *Callorhinus*. Allen and Bryant (1870) presented drawings of the skulls of young and adult *Callorhinus* and the first description of fur seal permanent dentition.

Allen (1880) stated that the teeth of *Callorhinus* are weaker than those of the southern fur seal *Arctocephalus*, the Steller sea lion *Eumetopias*, or the California sea lion *Zalophus*.

Note.—Approved for publication February 8, 1963.

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Kükenthal (1894) reviewed the literature on deciduous teeth of seven phocids and one otariid (the southern fur seal). In all he reported three deciduous premolars antecedent to the 2d, 3d, and 4th permanent premolars in each quadrant.

Lucas (1899) gave the deciduous and permanent dental formulas of *Callorhinus* as known today. He examined only one fetus younger than full term and identified as premolars the first four postcanines in each quadrant, after observing that the three deciduous premolars are adjacent to the alveoli of the 2d, 3d, and 4th permanent premolars.

Osborn (1907, p. 143) believed that "the teeth of the . . . Pinnipedia are so much modified secondarily that until we trace their ancestral history we cannot feel any confidence in attempts either to homologize the cusps or to trace these teeth back to a tritubercular or triconodont stage."

Todd (1918, p. 175) stated that "it does not take very long, geologically speaking, for a tritubercular molar to retrogress into a simple conical tooth." His remarks on the California sea lion *Zalophus* apply also to *Callorhinus*: "The premolars and molar of the maxilla are secondarily simple teeth, each with a well-marked cingulum surrounding the base of the crown. Their single cusps probably represent the paracone. The mandibular cheek teeth are also simple but the basal cingulum rises into a small cusp in front and behind the apex [crown tip] of the tooth, which may be the homologue of the protoconid" (p. 186).

Kellogg (1922) concluded that the terrestrial ancestors of the Pinnipedia may have had six more teeth than has modern *Callorhinus*. They may have had, on each side, one more upper posterior molar, one more lower medial incisor, and one more lower posterior molar. "In studying the dentition of the Otariidae," wrote Kellogg (p. 64, 100), "the fact is gradually forced upon one that the earliest otarids slowly retrogressed from the complex, flesh-tearing dentition of the land carnivores and reverted back toward a simple, conical tooth most favorable for the capture of elusive prey. . . . The evidence shows that the reduction of the true molars was very rapid in the Otariidae, at least."

Howell (1929) gave a dental formula for otariids which included one, two, or three lower molars on each side. Reference to three lower molars is puzzling. While the Miocene pinniped *Allodesmus* had two lower molars, no modern pinniped normally has more than one on each side.

Simpson (1945, p. 233) stated that "probably the pinnipeds are an early offshoot of the little differentiated late Eocene and early Oligocene canoid ancestry, paralleled by the otters, which had the same ultimate origin and a similar adaptive trend, and in other features by the bears, also with the same remote origin." The oldest known pinniped remains are from Miocene beds, perhaps 35 million years old. The remains are fossil skulls and skeletons, and are obviously those of pinnipeds. Their progenitors are completely unknown (Scheffer, 1958).

Rand (1950) studied the dentitions of 42 pups of the southern fur seal *Arctocephalus*. The teeth are like those of *Callorhinus*, although deciduous canines may persist for 5 months and deciduous premolars for 4 months after birth.

Gregory (1951, p. 405) stated that the teeth of seals "are usually 'simple' pegs, with a basal cingulum, a small basal cusp and conical, slightly recurved crowns adapted for fish-catching. Very probably this is a retrogressive, secondarily simplified dentition." He stated that there are four premolars in each quadrant, and he supposed that all have deciduous predecessors.

In a random sample of 38 female fur seal skulls, Chiasson (1955) found 6 that lacked one or more upper teeth, usually including the posterior upper molar. He stated (p. 564) "due to the fact that fur seals may replace the 6th upper postcanine [m2], this deciduous tooth might, upon accidental extraction, be replaced by the permanent tooth."

In 1957 Chiasson presented a discussion of the dentition of the fur seal. He emphasized the "double-rooted tooth development" of the posterior postcanines, stating that it "appears in the alligator and perhaps in other reptiles but not, to my knowledge, in any other mammal." Chiasson implied that the fur seal can have only three premolars in each half of each jaw since it has only three deciduous postcanines. He surmised that pinnipeds could not have evolved from creodont (precarnivore) stock because the creodonts had complicated teeth and modern seals do not.

Sergeant (1959) and Laws (1962) discussed the rhythmic deposition of dentin and cementum on the teeth of seals and cetaceans. The result is often a series of annual growth layers or ridges, useful as indicators of age (see page 308).

An Interim Convention on Conservation of North Pacific Fur Seals was signed in 1957 by representatives of four nations. The Convention resulted in anatomical studies by biologists of Canada, Japan, and the United States. The studies have produced six recent reports on dentition, namely, theses by Bokstrom (1961), Takano (1961), and Lamb (1962), written with the guidance of Kraus; and three publications by Kubota, Komura, Nagasaki, Tsuboi, and Matsumoto (1961a, b) and Kubota, Nagasaki, Matsumoto, and Tsuboi (1961). We shall discuss these later.

In critically reviewing previous research, the following points are important: (1) The number of permanent premolars in each quadrant has been given, variously, as three and four; four is correct. (2) In the southern fur seal, the deciduous canines may persist for 5 months, as against 3 months in the northern genus (p. 300). (3) While fossil evidence is lacking, the teeth of pre-Miocene seals were presumably more numerous and were more elaborately cusped than those of Recent seals. (4) One author has emphasized the evolutionary importance of the simple crown of all postcanines, and the double root of certain postcanines. In our opinion, there has been ample time—at least 35 million years—for the development of both features. (5) From six recent reports issued in 1961 and 1962, pertinent data have been extracted and will be used in the present paper as supplementary and comparative material, with appropriate citations.

MATERIALS AND METHODS

Numbers of Specimens

The specimens of the present study were collected on the Pribilof Islands, or at sea along the northwest coast of North America. They include material in formalin, dry skulls, dental arches only, isolated teeth, and photographs only, as follows:

	Number
Fetal and prematurely born (aborted)	20
Newborn and full-term fetal	18
Pups older than newborn	34
Yearling, pelagic	5
Yearling, autumn (on land)	4
Ages 2 to 10 years	62
Over 10 years	24
Total	167

Of these, about half are represented by skulls in the permanent collection of the National Museum or in the Bureau of Commercial Fisheries Marine Mammal Biological Laboratory. The others are represented by specimens which have been dissected, photographed in the field, or otherwise treated as temporary study materials.

We have also examined, in order to estimate the incidence of anomalous teeth, the skulls of 42 seals taken pelagically in 1952, and several hundred isolated teeth (right upper canines) taken in the course of fur seal population studies.

Dr. Tadahiro Ohe (Tokyo Medical and Dental University), while studying at the University of Washington School of Dentistry in 1962, made special preparations of several early fetuses and has generously allowed us to use certain of his unpublished findings. These are noted at appropriate places.

With minor exceptions, the specimens represent seals killed at random from a normal population. They do not represent a pathological group or a group of individuals found dead and salvaged for scientific use. The demonstrated variability in dentition is believed to be typical of the population at large.

Ages of Specimens

The exact ages of the fetal specimens are not known. From embryological evidence, however, it is possible to estimate for a fetus of given weight, its implanted age and its progress toward full-term size. The evidence is sketched below.

Date of implantation.—Pearson and Enders (1951) examined the genital tracts of 99 adult female seals killed on a Pribilof breeding ground on October 27, 1949. The seals were 4 years old or older. In each of 10 tracts the investigators found a single blastocyst, and they noted that around 6 of the blastocysts an implantation pocket was beginning to form. The general conclusion may be drawn that, by late October at least, no embryo of macroscopic size is present.

Scheffer (1960) examined another collection of adult female tracts obtained on the same breeding ground, though later in the year, as follows: four tracts on November 18, 1958, three tracts on 28 November 1951, and five tracts on December 3, 1958. Only in the December sample did he find embryos of macroscopic size: three embryos 10, 10, and 20 mm. in crown-rump length.

Douglas G. Chapman (in letter of October 15, 1957) analyzed the weights of 398 fetuses collected between mid-January and the end of June. The weights "were plotted on arithmetical probability paper (time versus percent of final value). This is essentially equivalent to assuming that the growth curve follows the logistic form." Extrapolation suggested a fetal weight of 10 g. for both male and female on November 21. Considering all the evidence available, we tentatively conclude that the mean date of implantation is in mid-November.

Fetal growth rate.—The weights of the 398 fetuses have been published (Scheffer, 1962). A chart of the weights up to the 10-day period centering on June 28 is shown in figure 1. During this last period, the mean weight of four males was 5.6 kg., and of seven females was 5.5 kg.

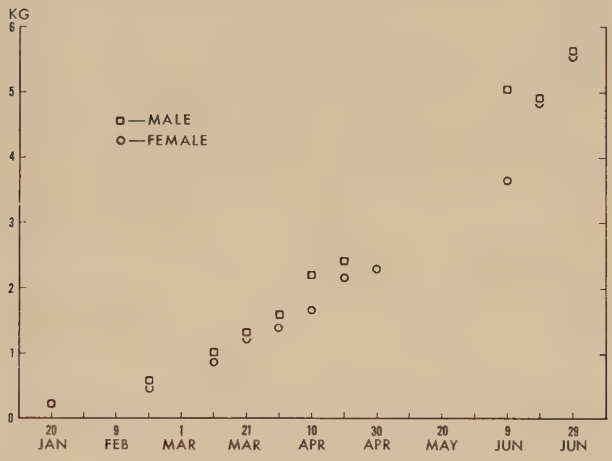

FIGURE 1.—Body weight of the fetal male and female, January to June. (Based on the weights of 209 males and 189 females (Scheffer, 1962, tables 1 and 2).)

Date of birth and weight of the newborn pup.—On a breeding ground where at least 782 pups were born in the summer of 1951, Bartholomew recorded the number born per day (Bartholomew and Hoel, 1953). The mean birth date was July 13.

At various times in summer on the breeding grounds, a total of 39 newborn and full-term fetal pups have been weighed (Scheffer and Wilke, 1953). The mean weight of 23 males was 5.4 kg., and of 16 females, 4.8 kg. These values are slightly less (7 percent) than those obtained for 11 fetal seals collected at sea in late June (see above). The discrepancy is probably a small-sample effect, though perhaps it may also be due to natural variation, from one year to the next, in newborn size. For purposes of the present paper, mean newborn weight (MNW) is 5.4 kg. for males and 4.8 kg. for females.

Ages of postnatal specimens.—From the time it is born in midsummer to the time it departs from land in late autumn, a pup, or individual in the calendar year of its birth, is identifiable as such. At birth it wears a distinctive black pelage. By age 3 months, the black coat has been replaced by a silvery, adult-type pelage. At this stage the pup can be distinguished in the field from a yearling by its smaller size and less prominent canine teeth. We will show (table 15) that the length of the upper canine root is only 3 mm. in the late autumn pup as against 9 mm. in the yearling. Between the pup and the yearling there may be some overlap in body weight and length, but apparently none in erupted length of the canines.

The ages of many specimens older than pups have been estimated quite closely from counts of annuli on the roots (Scheffer, 1950). The exact ages are known for other specimens which had been captured, marked, and released during their first summer and recaptured in later years. Through 1962, about 527,000 pups had been marked on the Pribilof Islands by a permanent metal tag clamped to a flipper.

Dental Terminology

Dental terminology for the fur seal and, indeed, for many mammals including man, is still controversial. The terminology used in the present paper is described below.

Primary tooth (indicated by small letter).—A tooth without a fetal antecedent.

Secondary tooth (indicated by large letter).—A tooth which develops near the locus of, and eventually replaces, a primary tooth.

Deciduous tooth.—A tooth which is exfoliated in utero or before age 14 weeks. All deciduous teeth are primary.

Permanent tooth.—A tooth which is normally retained through life. Most permanent teeth are secondary; certain ones are primary. During perinatal life while certain teeth of both deciduous and permanent series are present in the oral cavity the dentition is referred to as mixed.

Classified on the basis of their position in the dental arch, the permanent teeth are of four types.

Starting with the midline, the following teeth are present in each quadrant:

Incisors (I).—The most anterior teeth; rooted in the premaxillary bone (=intermaxillary bone=incisive bone) or mandibular bone; aligned approximately in a right-and-left (transverse) direction.

Canine (C).—The large tooth at the anterolateral corner of the jaw; rooted in the maxillary or mandibular bone.

Premolars (p and P).—The first four postcanines; rooted in the maxillary or mandibular bone.

Molars (m).—The most posterior teeth, being the 5th and 6th upper postcanines and the 5th lower postcanine; rooted in the maxillary or mandibular bone.

The deciduous teeth bear the names of the teeth which replace them.

The surfaces of the teeth are designated as:

Lingual.—That surface which is in contact with the tongue.

Labial.—That surface of the incisors which is in contact with the lips.

Buccal.—That surface of the canines and postcanines which is in contact with the cheek.

Occlusal.—That surface which comes into contact with the opposing teeth.

Mesial.—That surface which contacts (or nearly contacts) the tooth anterior to it in the dental arch.

Distal.—That surface which contacts (or nearly contacts) the tooth posterior to it in the dental arch.

The crown is the exposed, enamel-covered portion of the tooth. Near the gingival line, the enamel may form a shelf-like ridge or cingulum around the base of the crown. The neck is the region of the cementoenamel junction. The root s normally the hidden, cementum-covered portion of the tooth. The basal or apical end of the tooth s the attached end; the opposite end is usually referred to as the tip of the crown. The tooth s rooted in a socket, the bony alveolus.

Height of tooth is measured from the tip of the crown to the midpoint of the buccal or labial rim of the bony alveolus (=alveolar height= morphological height) or to the rim of the gingiva =gingival height), along the outer surface of the ooth. Special cases are: (1) on upper incisors 1 and I2, the tip of the crown is considered to be he more anterior of the two cusps; (2) for each anine, the measurement line is along the antero-ateral "prow"; (3) where the root of the molar is ongitudinally furrowed, a small peak of bone ay extend into the furrow, toward the crown, rom the bony alveolar rim, particularly on old eals; this peak is ignored in measuring alveolar height. A value given for "height" is the mean height of right and left teeth of a pair.

Length of root is measured on the extracted tooth, on the lingual surface from the cementoenamel junction to the base (apex). If the tooth is double-rooted, the mean length of the two roots is given. On canines, especially, the lingual surface is identified by a distinct "keel" that runs the length of the crown.

Condylobasal length (CBL) is measured from a transverse line touching the most posterior points on the occipital condyles to a transverse line touching the most anterior points on the premaxillary bones. In other words, it is a midline measurement between a tangent to the most posterior points of the condyles to the most anterior points of the midsagittal plane of the premaxilla. On fetal skulls having a CBL of less than 75–80 mm., the condyles slope into the parietal region and the "most posterior points" are difficult to identify.

Cranial width (CW) is calvarial width, or the greatest transverse width of the brain case posterior to the zygomatic arches. In males, it exceeds mastoid width until ages 4 to 6 years, when mastoid width overtakes it. Thus, in fully adult males, cranial width equals mastoid width. In females, cranial width is always greater than mastoid width. Scheffer and Wilke (1953) defined and illustrated mastoid width as the greatest width of the skull across, "or near," the mastoid processes. Modern opinion is that the term mastoid width should be restricted to the width across the processes.

Length of postcanine series is measured on a straight line along the axis of the tooth row from the distal (posterior) margin of the bony alveolus of the posterior molar to the mesial (anterior) margin of the bony alveolus of the anterior premolar.

The principal events that we shall be concerned with in the development of the dentition are as follows: Crown calcification, or formation of enamel and dentin, begins in deciduous and permanent teeth in early fetal life. Root formation begins in each tooth before crown calcification has ceased. Growth of the root is accompanied by alveolar eruption, when the tip of the crown rises above the bony alveolar rim, and later by gingival eruption (=clinical eruption) when the tip cuts the gum and enters the oral cavity. Root closure, or closure of the apical foramen, is followed by exfoliation (=shedding) in the deciduous teeth. Root closure in the permanent teeth is apparently followed by slow deposition of cementum; the teeth remain in place. (In the development of the deciduous dentition of the fur seal a curious and unexplained sequence is observed. In all teeth except the canines, root closure takes place a week or more in advance of gingival eruption.)

DECIDUOUS TEETH

Morphology of Deciduous Teeth

The deciduous formula (plates 1 and 2) is:

$$\frac{\text{i1—i2—i3 c p2—p3—p4}}{\text{i2—i3 c p2—p3—p4}}$$

The deciduous teeth are small and, excepting the canines, are nonfunctional. They are haplodont (with simple crown), though the premolars have small anterior and posterior bulges suggesting cusps. All are weakly rooted; some occasionally do not erupt from the gum; none remains after the first 13 weeks of the 3- to 4-month suckling period. Excepting those of the canines, the roots attain full size in utero. In the dentitions of two fetal males and two fetal females, ranging in body weight from 1.36 to 2.27 kg. (25 to 42 percent MNW), the following teeth are found to be double-rooted; upper p2, upper p4, and lower p4. The others are single-rooted. Kubota et al. (1961b) reported a similar finding.

Calcification, Alveolar Eruption, and Root Closure of Deciduous Teeth

Calcification.—Takano (1961), who studied stained sections and radiographs, found that the lower deciduous teeth "begin calcifying after 1 percent MNW (mean newborn weight). All of the [lower] deciduous teeth showed calcification before 2.1 percent MNW in the female and 2.4 percent MNW in the male" (p. 25).

Lamb (1962) determined the time of appearance of both dentin and enamel in the deciduous teeth of the lower jaw (table 1). His findings agree with Takano's, that calcification of all lower deciduous teeth is initiated before or soon after the fetus has attained 2 percent MNW.

TABLE 1.—*Presence of dentin and enamel in the mandibular dentition of the fetus* [1]

[For dental terminology used in this and subsequent tables, see pages 296 to 298]

Teeth	Weight of fetus, as percentage of mean newborn weight				
	1 percent	2 percent	3 percent	4 percent	5 percent
	Presence of dentin and enamel [2]				
Deciduous:					
i2	—	DE	DE	DE	DE
i3	—	D	DE	DE	DE
c	—	D	DE	DE	DE
p2	D	DE	DE	DE	DE
p3	D	DE	DE	DE	DE
p4	D	DE	DE	DE	DE
Permanent:					
I2	—	—	—	—	—
I3	—	—	—	—	—
C	—	—	D	—	D
p1	—	—	—	D	D
P2	—	—	—	—	—
P3	—	—	—	—	—
P4	—	—	—	—	—
m1	—	—	—	—	—

[1] After Lamb (1962, p. 35) based on five male fetuses.

[2] D=dentin, E=enamel, identified by radiography and examination of stained frontal sections.

As for the upper deciduous teeth, the radiographs of Kubota et al. (1961b) show that the teeth calcify at about the same time as the lower ones. Those authors, however, did not give the weights of the fetuses nor did they indicate the sequence of calcification of the upper deciduous teeth, beyond stating that calcification starts in the incisors.

Takano (1961, p. 25) stated that "the deciduous . . . teeth do not form completely enclosed within bone" but, rather, "crown formation takes place within a soft tissue mass which is directly connected to the gingival tissue." In other words, all deciduous teeth except the canines develop in shallow depressions rather than in true bony alveoli. Lamb (1962) concluded that histodifferentiation during tooth formation in the seal is essentially the same as in man.

In summary, we conclude that crown calcification of the deciduous teeth is progressing while the fetus is increasing in weight from about 100 g. (2 percent MNW, implanted age about 7–8 weeks) to 150 g. (3 percent MNW, implanted age about 8–9 weeks), in January.

Alveolar eruption.—Alveolar eruption of the deciduous teeth has no distinct beginning, for the smallest teeth, the medial incisors, begin to calcify at the level of the bony alveolar rim. In our smallest specimen preserved as a cleaned skull, all deciduous teeth have erupted beyond the bony alveolar rim. This is a female of 438 g. (9.1 percent MNW). Here the tooth with least alveolar height (0.5 mm.) is the upper 4th premolar, and with the greatest alveolar height (2.2 mm.) is the upper 3d incisor.

TABLE 2.—*Alveolar height of deciduous teeth*

Teeth	Specimen catalog number[1]						
	39	40	34	41	36	37	29
	Alveolar height (mm.)						
Upper:							
i1	1.0	1.0	1.0	0.5	lost	1.3	1.0
i2	1.0	1.2	1.0	1.0	1.6	1.3	1.0
i3	2.6	1.6	2.6	2.0	1.9	2.2	2.7
c[2]	4.2	4.3	4.3	5.0	4.8	4.6	4.6
p2	2.0	2.1	2.3	3.1	2.6	2.6	2.9
p3	1.7	1.3	2.5	2.2	2.2	2.0	2.2
p4	1.8	2.2	2.6	2.5	2.1	2.2	2.5
Lower:							
i2	1.0	1.9	0.8	1.0	2.0	1.5	lost
i3	1.0	2.2	1.0	2.0	2.7	1.5	3.0
c[2]	3.3	3.2	3.0	3.5	3.4	3.1	4.1
p2	2.7	2.1	2.6	2.9	2.6	3.0	3.1
p3	2.0	2.2	2.5	1.9	2.0	2.8	2.5
p4	2.3	2.2	2.3	2.3	2.3	2.4	2.5
Total tooth heights	26.6	27.5	28.5	29.9	30.2	30.5	32.1
	Specimen data						
Sex	Male	Female	Male	Male	Male	Female	Female.
Date	Mar. 30	Apr. 1	Mar. 28	Apr. 1	Mar. 30	Mar. 30	Mar. 28.
Condylobasal length, mm	72	79	85	90	81	84	85.
Body length, cm	40	41	42	47	42	42	43.
Body weight, kg	1.4	1.4	1.8	2.3	1.8	1.6	1.8.
Percent MNW	25	28	33	42	33	33	38.

[1] All specimens are in the "Sitka 50" series; all are fetal and are listed according to increasing total tooth height.

[2] The canines continue to grow in perinatal life. Maximum recorded heights are: upper, 8.2 mm; lower, 5.5 mm.

In a slightly larger fetus (female, 660 g., 13.7 percent MNW) alveolar eruption of the deciduous teeth is also complete. For seven still larger specimens, the alveolar height of each tooth is shown in table 2.

We conclude that alveolar eruption begins shortly after crown calcification in the fetus of 200 g. (4 percent MNW, implanted age about 10 weeks), and has begun in all teeth in the fetus of 400 g. (8 percent MNW, implanted age 12–13 weeks), in January and February.

Root closure.—In a fetal male of 1.36 kg. (25 percent MNW) the root of upper c is open; the roots of upper i1, i2, and p4 are nearly closed; the roots of upper i3, p2, and p3 are closed; the roots of lower c and p4 are open; the roots of lower i2, i3, p2, and p3 are closed. In two fetal females of 1.36 and 1.59 kg. (28 and 33 percent MNW) all roots are closed except those of upper and lower c plate 2).

We conclude that, in certain deciduous incisors and premolars, the roots close when the fetus has attained a weight of about 1.0 kg. (20 percent MNW). In the remaining incisors and premolars, the roots close when the fetus has attained a weight of about 1.50 kg. (30 percent MNW), when the first teeth are about to erupt from the gum. In the canines, the roots close near time of birth, earlier in the lower pair than in the upper.

Gingival Eruption of Deciduous Teeth

In two fetuses similar in appearance, both 1.35 kg. (27 percent MNW), no teeth have erupted from the gum, though the site of each tooth is evident as a mound. Two larger fetuses present a similar picture, with teeth unerupted, though by now the upper medial incisors (i1) show through the gingival tissue as slender dark lines, and in a 1.70 kg. specimen (34 percent MNW) lower i2 is about to erupt (plate 3).

The next fetus in size (2.3 kg., 45 percent MNW) is the first-listed of table 3. Here 9 teeth out of 26 have erupted. The specimens of table 3, collected between April 21 and July 5, suggest, but do not show clearly, the sequence of eruption. We have, therefore, rearranged the data of Kubota et al. (1961a, p. 330–333), based on 25 fetal specimens, mainly collected in April when eruption is most active. The sequence of eruption is as follows:

Upper:	i1	i2	i3	c	—	p2	p3	p4
Sequence:	7	11	3	1		2	6	8
		4	13	5		10	12	9
Lower:	—	i2	i3	c	—	p2	p3	p4

TABLE 3.—*Gingival eruption of deciduous teeth*

Teeth	Specimen catalog number [1]			
	NWC 52 3119	NWC 52 3122	NWC 52 3121	US 58 790 R
	Stage of eruption [2]			
Upper:				
i1	(x)	(x)	(x)	(x)
i2	/	(x)	(x)	(x)
i3	x	o	x	(x)
c	/	x	x	x
p2	/	x	x	x
p3	—	—	x	x
p4	—	—	o	x
Lower:				
i2	o	(x)	(x)	(x)
i3	(x)	(x)	(x)	(x)
c	—	o	x	x
p2	—	—	x	x
p3	—	—	—	x
p4	—	—	x	x
	Specimen data			
Age	Fetal	Fetal	Fetal	Fetal.
Sex	Female	Female	Male	Female.
Date	April 21	April 21	April 21	May 9.
Condylobasal length, mm	97	96	105	108.
Body length, cm	46	50	51	54.
Body weight, kg	2.3	2.4	2.7	3.4.
Percent MNW	45	50	50	71.

TABLE 3.—*Gingival eruption of deciduous teeth*—Con.

Teeth	Specimen catalog number [1]				
	26-6-60 A	5-7-60 A	BDM 549	NWC 52 3214	29-6-60 A
	Stage of eruption [2]				
Upper:					
i1	(x)	(x)	(x)	(x)	(x)
i2	(x)	(x)	(x)	(x)	(x)
i3	(x)	(x)	(x)	x	(x)
c	x	x	x	x	x
p2	(x)	(x)	(x)	x	(x)
p3	(x)	(x)	(x)	x	(x)
p4	/	x	x	x	x
Lower:					
i2	(x)	(x)	(x)	(x)	(x)
i3	(x)	(x)	(x)	(x)	(x)
c	x	/	x	x	(x)
p2	(x)	(x)	(x)	x	(x)
p3	(x)	(x)	(x)	x	(x)
p4	(x)	/	x	x	x
	Specimen data				
Age	Newborn	Newborn	Days?	Fetal	Fetal.
Sex	Female	Male	Male	Male	Female.
Date	June 26	July 5	July	June 20	June 29.
Condylobasal length, mm	122	124	135	132	133.
Body length, cm	65			66	69.
Body weight, kg	4.4		6.5	6.8	7.1.
Percent MNW	92		120	126	147.

[1] Specimens are listed in order of increasing weight or condylobasal length.
[2] Symbols: Dash (—)=tooth not erupted; o=tooth about to erupt; /=one tooth of a pair erupted; x=both teeth of a pair erupted; (x)=erupted but exfoliated.

We conclude that gingival eruption of the deciduous teeth is progressing while the fetus is increasing in weight from 1.65 kg. (33 percent MNW, implanted age about 20 weeks) to 3.0 kg. (60 percent MNW, implanted age about 25 weeks), in April and May. Eruption does not proceed in an anterior to posterior direction, as in the permanent teeth. The upper deciduous teeth tend to erupt slightly in advance of the lower ones. For reasons undetermined, all of the teeth except the canines erupt after root closure has taken place.

Exfoliation of Deciduous Teeth

Table 3, which shows gingival eruption, also indicates when certain teeth exfoliate.

The incisors, first to exfoliate, are usually shed before birth, perhaps as a result of "mouthing" movements of the fetus. They begin to exfoliate soon after the onset of gingival eruption. However, in the jaws of a fetal individual of 3.4 kg. (71 percent MNW) one incisor (left upper i2) is still attached to the gum. In the jaws of a newborn male, one lower i3 is persistent. In the jaws of a male a few days old, upper i1 can be seen as a white speck on the surface of the gum, most of its length buried.

The premolars (p2, p3, and p4) disappear just before or soon after the pup starts to nuzzle and suck. In six specimens including late-term fetuses and newborn young, only one, a large full-term fetus, has retained all of its deciduous premolars. A male several days old has retained only the posterior pair (p4) in upper and lower jaws.

The canines are far more deeply rooted than are other deciduous teeth and are functional after birth, the upper ones for a longer period than the lower ones. In our sample, the maximum alveolar height of upper c is 8.2 mm. in a male about 2 weeks old. Maximum height of lower c is 5.5 mm. in a full-term fetal male. One or more deciduous canines are present in 5 out of 14 skulls of known-age pups ranging in age from 23 to 103 days, as follows:

Age in days	Deciduous canines present (X)			
	Upper right	Upper left	Lower right	Lower left
23	X	X	X	X
23	X	X	X	X
25	—	—	—	—
32	—	—	—	—
39	—	—	—	—
50	—	—	—	—
63	—	—	—	—
66	—	—	—	—
66	—	—	—	—
73	X	X	—	—
73	—	—	—	—
83	—	—	—	—
92	X	—	—	—
103	—	—	—	—

The status of exfoliation near time of birth is hown in plate 4, and is indicated in table 3 by he data for the five last-listed individuals. These nclude two full-term fetuses, one pup on the day f its birth, and two pups a few days old. The deciduous teeth present or absent in each upper and lower quadrant are as follows:

Number of—	Upper (full complement 7 teeth)	Lower (full complement 6 teeth)
'eeth exfoliated	2–5.5 (mean 4.5)	2–5 (mean 4.2).
'eeth in situ	1.5–5 (mean 2.5)	1–4 (mean 1.8).

We conclude that exfoliation may begin in the etus of 2.0 to 2.5 kg. (40 to 50 percent MNW, mplanted age 22 to 24 weeks), in April and May. By time of birth, about 18 of the 26 teeth have exfoliated. The four posterior premolars (p4 in each quadrant) usually persist for a few days after birth. The four deeply rooted canines begin to exfoliate within a week or two after birth; all have been shed by age 14 weeks.

Evolutionary Implications

From modern embryological evidence the evolution of the deciduous dentition in *Callorhinus* may hypothetically be reconstructed, as follows: The protopinniped lived in a den near the sea or a brackish lagoon. The food of the growing individual was at first milk, then milk-plus-flesh, and finally flesh alone. As members of the evolutionary line began increasingly to exploit the advantages of a marine environment, the den life of the individual became shorter. Concurrently, a ong gestation period began to gain survival value, ince mutations in the direction of greater precocity at birth resulted in a pup which was sooner ble to leave the den and join its mother in the ood-rich waters. Today, the deciduous or "den" eeth, essentially nonfunctional, persist in the ntogenetic sequence, while gestation is now so xtended that the permanent teeth have time o develop in utero and be ready to meet a sudden emand at prenatal age of 3 or 4 months. At this tage, around the first of November, the mother eal leaves the nursing ground for the open sea. he pup is forced to convert abruptly from a diet f milk to one of fish and squid. (Or so we believe. ertainly the pup receives no milk after its mother ails to return periodically to the beach. No tomachs of pups taken at sea before January have yet been examined. We can only assume that the diet of the pelagic young seal in November and December is similar to that observed for seals in January and later.)

We do not wish to leave the impression that the deciduous teeth of the protopinniped have remained essentially unchanged in form, size, and number. On the contrary, evidence suggests that the teeth have become smaller, simpler in form, and more weakly rooted. Certain incisors have almost disappeared; presumptive lower "i1" has disappeared without trace. Nor do we wish to leave the impression that the fetal time gap between development of the deciduous and permanent teeth has remained unchanged. As we will point out in the next section, there has apparently been a fetal telescoping with the result that calcification of permanent teeth now begins when the fetus has attained only 3 percent of its ultimate newborn weight, and while calcification of certain deciduous teeth is still being initiated.

PERMANENT TEETH

Morphology of Permanent Teeth

The permanent formula (plates 5 to 7) is:

$$\frac{\text{I1—I2—I3}}{\text{I2—I3}}\quad\frac{\text{C}}{\text{C}}\quad\frac{\text{p1—P2—P3—P4}}{\text{p1—P2—P3—P4}}\quad\frac{\text{m1—m2}}{\text{m1}}$$

The incisors.—Pinnipeds (Order Pinnipedia) have fewer permanent incisors than do carnivores (Order Carnivora). The incisor formulas for members of the Pinnipedia are as follows:

Family Otariidae (on each side)	3/2
Family Odobenidae	3/2
Family Phocidae, Subfamily Phocinae	3/2
Subfamily Monachinae	2/2
Subfamily Cystophorinae	2/1

By comparison, all members of the Order Carnivora except the sea otter (*Enhydra lutris*) have three incisors on each side (3/3). It is assumed that, where pinnipeds have lost certain upper or lower incisors, they have lost the more medially placed ones and have retained the outer, more laterally placed ones (see formula at head of section).

For example, "in walrus [*Odobenus*] the first incisor, upper and lower, is certainly the smallest and least often present in both the deciduous and permanent dentitions" (Francis H. Fay, in letter of November 29, 1961). In the skulls of nine walrus calves, Fay[1] noted the frequency of occurrence of permanent incisors:

Incisors	I1	I2	I3
	Percent	*Percent*	*Percent*
Upper	56	78	100
Lower		22	66

In the skulls of 24 adults, however, he found no upper I1 and no lower incisors. He concluded that upper I3, the caniniform, is the only incisor consistently present in the adult, and that, in the evolution of the walrus, there has been a tendency toward absence of the medial rather than the lateral incisors.

Evidence for evolutionary loss of the lower medial incisors in *Callorhinus* is weaker. Unlike the walrus, the fur seal retains all of its permanent incisors through life. In the fur seal, however, in both deciduous and permanent dentitions and in both upper and lower arches, there is a gradient of incisor size decreasing in the direction of the midline. We agree with Kubota et al. (1961b, p. 393) that "the lower tooth opposite to the most rudimentary upper central incisor . . . has been lost."

The first two upper incisors (I1 and I2) on each side are notched transversely to accept the crown tips of the two lower incisors, which are chisel-shaped (plate 7). To the best of our knowledge, no members of the Order Carnivora have notched incisors, whereas all members of the Family Otariidae of the Order Pinnipedia do. When the seal's mouth is closed, the incisors, as well as other teeth, interlock to form a tight-fitting trap from which small fish or squid would have difficulty in escaping. The lower medial incisors (I2) are essentially tricuspidate (plate 8, *A*). The cusps become worn within a few weeks after birth and are not conspicuous in the adult. The incisors are usually single-rooted. We have seen only one specimen in which upper I1 and I2 are double-rooted (plate 9, *A*).

The canines.—The canines are like those of the Carnivora, with simple pointed crown and single root. We will discuss later (p. 308) the protracted growth period of the canine roots.

The postcanines.—The permanent molariform teeth, six postcanines in each upper quadrant and five in each lower, are superficially alike. We designate the most anterior four above and below as premolars, the rest as molars, for these reasons: (1) On histological evidence there is a discontinuity between the 4th and 5th postcanines, above and below, in the sense that the 4th is a secondary tooth while the 5th is a primary. (2) In eruptive sequence the upper first four (p1, P2, P3, and P4) fall in one group, the fifth (m1) in another. That is, in each upper quadrant the first four postcanines erupt from the gum in regular order, from anterior to posterior, but the 5th erupts out of turn, earlier than the 4th. (3) In the Superfamily Canoidea, nearest relatives of the Pinnipedia, the first four postcanines have long been regarded as premolars (Frechkop, 1955; Grassé, 1955; Gregory, 1951; Weber, 1928).

To elaborate on point 1 (above), the first upper and lower postcanine (p1), the 5th and 6th upper postcanines (m1 and m2), and the 5th lower postcanine (m1) are primary teeth. They have no surviving (functional) successors, though during fetal development each is paired for a short time on its lingual margin with the anlage of a secondary tooth (Tadahiro Ohe, in a letter of July 25, 1962).

Each postcanine may have a small anterior and a small posterior cusp or cusplet (plate 8, *B*). A carnassial (shearing) cusp is never found as on certain posterior teeth, usually the 5th upper and 4th lower postcanines, of Carnivora. A cingulum is conspicuous only on the postcanines of the seal, especially on the lingual side of the teeth.

The roots of the first three premolars (p1, P2, and P3), upper and lower, have a vertical groove which tends to be deeper in the posterior series o teeth. Upper m1 is nearly always double-rooted; lower m1, usually; upper m2 and upper and lowe P4, occasionally (tables 4 and 5; plate 9, *B*). There is no apparent sex difference in shape o root of the postcanines. (Tables 4 and 5 are based on specimens 8 years old or younger. Above 6 to 8 years, unless the root is distinctly bifurcated, cementum deposition tends to obscure the original shape.)

The posterior upper tooth, m2, is consistently the smallest of the molariform teeth, and it has no antagonist. It may be absent without trace from adult skulls (p. 311). The root of m2 turn

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[1] Investigations of the Pacific walrus. Terminal report, Project No. 26, Arctic Institute of North America, March 1960, 3+72 typewritten pages.

TABLE 4.—*Shape of root in permanent posterior postcanines, male*

Catalogue No.	Age of specimen	Upper teeth			Lower teeth	
		P4	m1	m2	P4	m1
		Shape of root [1]				
DM 417	9 months	D	C	D	D	D
DM 476	14 months	D	A	A	D	C
DM 290	14 months	C	A	C	C	C
DM 552	2 years	D	A	A	C	A
-7-60A	2 years	D	A	B	D	C
DM 50	3 years	D	A	D	D	A
DM 53	3 years	C	B	C	D	C
DM 51	4 years	B	A	B	D	A
DM 68	4 years	A	A	C	A	A
DM 107	5 years	C	A	C	C	B
DM 149	6 years	C	A	B	D	B
Mean score [2]		3.2	1.3	2.5	3.4	2.2

[1] Symbols: A=root double and distinctly bifurcated; B=root double but ot distinctly bifurcated; C=root deeply furrowed but not double; D=root ngle, not furrowed.

[2] The tooth which is most consistently double-rooted has the lowest score, ased on a system where A=1, B=2, C=3, and D=4.

TABLE 5.—*Shape of root in permanent posterior postcanines, female*

Catalogue No.	Age of specimen	Upper teeth			Lower teeth	
		P4	m1	m2	P4	m1
		Shape of root [1]				
DM 545	7 months	D	A	B	D	C
DM 16	15 months	C	A	B	D	B
DM 407	2 years	C	A	D	D	A
WC 52-3097	3 years	C	B	C	C	C
DM 405	3 years	C	A	A	D	B
WC 52-3632	5 years	B	A	B	C	A
DM 460	5 years	C	A	B	B	B
WC 52-3661	7 years	B	A	D	B	A
DM 463	7 years	B	A	D	A	A
WC 52-3272	8 years	B	A	D	B	C
Mean score [2]		2.7	1.1	2.8	2.9	1.9

[1] Symbols: A=root double and distinctly bifurcated; B=root double but ot distinctly bifurcated; C=root deeply furrowed but not double; D=root ngle, not furrowed.

[2] The tooth which is most consistently double-rooted has the lowest score, sed on a system where A=1, B=2, C=3, and D=4.

nteriorward, perhaps thereby securing a better old in the thicker part of the maxillary bone.

alcification and Alveolar Eruption of Permanent Teeth

Calcification.—Calcification of the permanent eeth starts in the lower canine at fetal weight of 50 g. (3 percent MNW, about 9 weeks implanted ge), in January. This is remarkably early com- ared with man. Kraus (1959) found that the rst human permanent tooth begins to calcify at bout time of birth, or 40 weeks implanted age, uch later than in the seal. The permanent 1st andibular molar of the rhesus monkey begins to lcify after the first three-quarters of prenatal evelopment (Swindler and Gavan, 1962). Possi- y this indicates a trend toward delayed cal- fication of permanent teeth in human evolution.

Initial calcification in the permanent dentition overlaps that in the deciduous, though is much more prolonged. That is, initial calcification is occurring in deciduous teeth at fetal stages of 2 to 3 percent MNW, while it is occurring in permanent teeth at fetal stages of 3 to 70 percent MNW. Initial calcification is last to start in the posterior upper molar, m2, in the fetus of about 3.5 g. (70 percent MNW, implanted age about 27 weeks) (Bokstrom, 1961; Takano, 1961; Kubota et al., 1961b; Lamb, 1962).

The sequence of calcification as described by Bokstrom, Takano, and Lamb was given separately for upper and lower teeth. We are unable to coordinate the sequence for the dentition as a whole, except to state that the lower teeth tend to calcify before their upper counterparts. Thus calcification has started in all of the lower teeth by fetal weight 0.9 kg. (18 percent MNW) as compared with 3.5 kg. (70 percent MNW) for the uppers. The sequence is as follows:

Maxillary	*Mandibular*
1. C and p1	C and p1.
2. I3 and m1	I2 and m1.
3. I1 and I2	P3.
4. P2, P3, and P4	I3 and P2.
5. m2	P4.

Alveolar eruption.—The sequence of alveolar eruption of the permanent teeth is difficult to demonstrate in our specimens, which are skulls cleaned by beetle larvae. In many skulls which ought to show the sequence of eruption, beetles have eaten the periodontal membranes around the partly formed teeth, allowing the loose teeth to sink into the alveoli. In the skull of a fetus of 660 g. (13 percent MNW), however, the following permanent teeth can be seen: upper canines and first three postcanines (p1, P2, and P3), lower canines and all five postcanines (p1, P2, P3, P4, and m1). All upper and lower incisors are hidden beneath dried remains of the gingiva. The last three upper postcanines (P4, m1 and m2) cannot be seen.

In a sample of seven older skulls taken from fetuses ranging in size from 1.36 to 2.27 kg. (25 to 42 percent MNW) all of the permanent teeth, except the posterior upper molar m2, are visible within their alveoli. The tips of their crowns are white, hard, and well calcified. From the stage of advancement of the tips we conclude that the first teeth—the incisors—erupt from the jaw when the fetus has attained a weight of about 2.5 kg. (50 percent MNW, implanted age about 24 weeks), in early May.

The status of alveolar eruption near time of birth is shown in table 6 and plates 10 and 11. All of the permanent teeth have usually erupted in utero to the level of, or beyond, the bony alveolar rim.

Alveolar eruption evidently continues through life. Increase in alveolar height between ages 5 and 10-plus years is shown in table 7. Table 7 suggests that, in the female, most of the teeth grow less than 1 mm. in root length after age 5 years. Exceptions are the large caniniform incisor (upper I3) and the canines. Alveolar height of the permanent teeth in fully adult skulls of both sexes is shown in table 8 and figure 2. The causes of increase in alveolar height during adult life are not clear, though cementum deposition on the roots is quite certainly one of them. Resorption of the bony alveolar rim is perhaps another (plate 20, A).

TABLE 6.—*Alveolar height of permanent teeth in fetal and newborn pups*

Teeth	Specimen catalog number [1]			
	BDM 325	BDM 547	BDM 225	BDM 450
	Alveolar height (mm) [2]			
Upper:				
I1	2.0	5.8	5.1	5.3
I2	2.0	5.6	5.5	6.0
I3	1.2	8.0	8.2	8.4
C	2.0	4.0	6.8	7.8
p1	1.9	4.7	6.9	6.9
P2	—	3.9	6.1	4.7
P3	—	3.9	4.0	4.6
P4	—	.8	3.5	2.4
m1	.2	3.6	4.3	4.1
m2	—	.8	—	2.0
Lower:				
I2	3.9	6.3	5.9	6.2
I3	2.9	6.3	6.2	7.0
C	.1	.1	7.0	6.9
p1	3.3	6.7	6.3	7.0
P2	1.0	6.6	6.0	6.6
P3	.2	7.0	6.2	6.4
P4	—	1.0	3.5	3.5
m1	.5	2.0	2.0	4.1
Total tooth heights	21.2	77.1	93.5	99.9
Specimen data				
Age	Fetal	Fetal	Days?	Days?
Sex	Female	Male	Female	Female.
Date	July 18	July 31	July 23	August 11
Condylobasal length, mm	99	122	123	121.
Body length, cm	49		67	67.
Body weight, kg	2.8	6.0	4.8	5.2.
Percent MNW	56	111	99	109.

[1] Specimens are listed by increasing total tooth height.
[2] A dash indicates an unerupted tooth.

TABLE 7.—*Alveolar height of permanent teeth in the female at ages 5 and 10+ years*

Teeth	Six specimens age 5 years			Seven specimens age 10+ years [1]			Difference between means (increase)
	Aleveolar height (mm)			Alveolar height (mm)			
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	
Upper:							
I1	6.3	7.7	6.95	7.0	8.6	7.85	0.90
I2	7.2	8.0	7.38	7.0	9.0	7.93	.55
I3	9.4	10.5	10.08	10.1	14.0	11.62	1.54
C	19.0	19.5	19.20	21.0	27.0	24.30	5.10
p1	7.8	9.8	8.78	8.7	10.9	9.47	.69
P2	7.3	9.0	8.33	8.3	9.7	8.94	.61
P3	6.7	8.5	7.77	7.4	9.2	8.21	.44
P4	6.3	8.0	7.48	7.2	8.6	8.09	.61
m1	6.1	8.0	7.03	6.2	9.0	7.81	.78
m2	6.3	7.0	6.73	5.5	9.0	7.27	.54
Lower:							
I2	6.4	7.3	6.95	6.5	7.9	7.18	.23
I3	6.9	8.2	7.25	7.0	9.0	7.63	.38
C	15.0	18.0	16.75	20.0	22.0	21.00	4.25
p1	7.0	8.8	7.77	7.6	9.8	8.56	.79
P2	6.2	8.8	7.90	7.6	9.1	8.40	.50
P3	7.1	9.1	8.57	8.2	10.0	9.34	.77
P4	7.1	9.1	8.25	7.8	9.3	8.67	.42
m1	6.3	8.1	7.42	7.7	9.6	8.63	.21

[1] For these old specimens, the height of the canine teeth has been "restored" by small amounts, averaging 1.1 mm, to eliminate the factor of crown-wear. The aim has been to show alveolar height as an indirect measure of root increase.

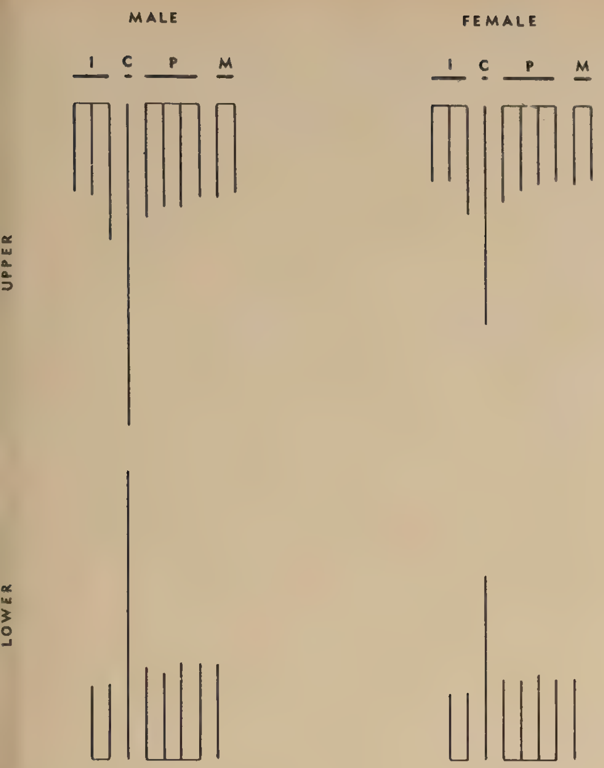
TABLE 8.—*Alveolar height of permanent teeth in the adult*

Teeth	Mean alveolar height of tooth (mm)	
	In seven males [1]	In seven females [2]
Upper:		
I1	9.9	8.5
I2	10.2	8.5
I3	15.1	12.2
C	36.0	24.5
p1	12.7	10.7
P2	11.6	9.4
P3	11.6	8.8
P4	10.4	8.6
m1	10.4	8.8
m2	9.9	8.3
Lower:		
I2	8.3	7.4
I3	8.3	7.5
C	32.2	20.7
p1	10.3	9.0
P2	9.7	8.9
P3	10.9	9.5
P4	10.7	9.0
m1	10.7	9.0

[1] The sample included one 9-year-old, three 10-year-olds, and three older than 10, though the value shown for each tooth is the mean of the highest three. By this expedient, an attempt is made to show the height of the fully grown, but yet unworn, tooth.
[2] The sample included three 9-year-olds, one 10-year-old, and three older than 10, though the value shown for each is the mean of the highest three.

Gingival Eruption of Permanent Teeth

We have measured the height of the teeth above the gum in the jaws of 9 male and 10 female pups ranging in age from full-term fetal to 103 days (tables 9 and 10). We have also measured gingival height in five fully adult males and five fully adult females (table 11). As a basis for estimating the sequence of gingival eruption (table 12), we have analyzed the data for the six youngest specimens listed in table 9.



IGURE 2.—Relative alveolar height of permanent teeth in the adult male and female. The length of each vertical bar represents the height of the tooth above the bony alveolar rim. The upper teeth are represented as pointing downward, the lower teeth as pointing upward. I=incisors, C=canines, P=premolars, M=molars. (Data from table 8.)

hese represent an important perinatal period nding when the last tooth (upper m2) is about erupt. One clue to the sequence is the number f specimens, in an age-graduated series, in which particular tooth is present in the oral cavity. hat is, a particular tooth present in six out of x specimens is assumed to have erupted earlier ian another which is present in only four out of ie same six specimens. A second clue is the uptive maturation, or progress of a particular ooth toward its adult height. That is, a tooth hich has already attained 80 or 90 percent of s estimated ultimate height is assumed to have upted earlier that one in the same specimen hich has attained only 60 percent of its estiated ultimate height. The estimated sequence of uption is as follows:

Upper:	I1	I2	I3	C	p1	P2	P3	P4	m1	m2
equence:	2	4	7	16	6	9	12	13	14	18
		1	3	15	5	8	10	11	17	
Lower:		I2	I3	C	p1	P2	P3	P4	m1	

TABLE 9.—*Gingival height of permanent teeth in the pup, male*

Teeth	Specimen catalog number [1]				
	BDM 549	5-7-60 A	NWC 52 3214	24-7-60 A	23-8-60 A
	Gingival height (mm) [2]				
Upper:					
I1	2.8	2.7	3.5	3.5	4.3
I2	2.8	2.8	3.2	3.7	4.4
I3	—	3.8	3.3	4.7	7.1
C	—	—	—	—	.2
p1	—	2.4	2.9	3.4	4.7
P2	—	.2	.2	.2	4.1
P3	—	—	—	—	2.0
P4	—	—	—	—	1.5
m1	—	—	—	—	2.0
m2	—	—	—	—	—
Lower:					
I2	2.3	2.2	3.4	2.5	3.2
I3	3.5	2.7	4.3	4.0	4.3
C	—	1.5	—	—	—
p1	2.4	.4	2.6	2.6	4.1
P2	.6	—	1.0	.8	4.7
P3	.2	—	.1	.3	4.6
P4	—	—	—	.8	1.8
m1	—	—	—	—	—
Total tooth heights	14.6	18.7	24.5	26.5	53.0
	Specimen data				
Age	Days?	Newborn	Fetal	Newborn	Days?
Date	July	July 5	June 20	July 24	August 23
Body length, cm			66		
Body weight, kg	6.5		6.8		
Percent MNW	120		126		

[1] Specimens are listed by increasing total tooth heights.
[2] A dash indicates an unerupted tooth.

Teeth	Specimen catalog number [1]			
	15-8-60 A	D 3 62	D 2 62	D 7 62
	Gingival height (mm) [2]			
Upper:				
I1	3.0	4.5	4.0	5.0
I2	3.7	4.7	4.5	5.5
I3	7.0	8.3	7.6	6.5
C	3.3	.3	4.0	7.2
p1	5.8	5.9	5.9	5.4
P2	3.3	5.0	5.8	6.9
P3	2.7	5.0	5.4	5.3
P4	1.2	4.3	5.6	4.5
m1	2.0	5.7	5.0	6.5
m2	—	.1	.5	1.0
Lower:				
I2	3.2	3.5	3.7	4.1
I3	4.1	5.0	5.0	5.6
C	3.9	.1	1.6	2.8
p1	3.8	4.2	4.3	4.2
P2	3.6	5.9	6.0	6.3
P3	2.7	5.3	6.2	6.0
P4	.9	2.5	3.0	3.9
m1	.2	2.6	1.0	1.7
Total tooth height	54.4	72.9	79.1	88.4
	Specimen data			
Age	Days?	73 days	66 days	103 days.
Date	Aug. 15	Sept. 9	Sept. 2	Oct. 9.
Body length, cm		72	69	80.
Body weight, kg		7.4	7.9	11.6.
Percent MNW		137	146	215.

[1] Specimens are listed by increasing total tooth heights.
[2] A dash indicates an unerupted tooth.

Table 10.—*Gingival height of permanent teeth in the pup, female*

Teeth	Specimen catalog number [1]				
	26–6–60 A	15–8–60 C	23–8–60 B	15–8–60 B	23–8–60 C
	Gingival height (mm) [2]				
Upper:					
I1	2.7	5.0	4.0	3.5	3.5
I2	3.3	5.0	4.4	3.6	3.8
I3	5.0	7.2	6.2	6.3	7.0
C	.2	—	3.1	6.0	4.8
p1	3.6	5.5	4.2	5.5	5.1
P2	2.0	3.3	3.2	4.4	4.4
P3	.1	3.2	2.0	2.9	3.2
P4	—	1.6	1.9	.2	2.6
m1	—	2.0	3.6	3.5	4.8
m2	—	—	—	—	—
Lower:					
I2	2.3	2.7	3.2	3.0	2.9
I3	2.7	3.7	4.3	3.8	3.7
C	3.0	—	2.7	5.3	5.6
p1	2.8	4.0	4.3	3.5	3.5
P2	2.9	4.4	4.1	4.4	4.4
P3	2.5	4.2	3.5	4.1	4.4
P4	—	1.4	1.3	1.5	3.0
m1	—	—	.1	—	1.9
Total tooth heights	33.1	53.2	56.1	61.5	68.6
	Specimen data				
Age	Newborn	Days?	Days?	Days?	Days?
Date	June 26	Aug. 15	Aug. 23	Aug. 15	Aug. 23
Body length, cm	65				
Body weight, kg	4.4				
Percent MNW	92				

[1] Specimens are listed by increasing total tooth heights.
[2] A dash indicates an unerupted tooth.

Teeth	Specimen catalog number [1]			
	D6 62	D1 62	D5 62	D4 62
	Gingival height (mm) [2]			
Upper:				
I1	4.5	3.6	4.0	4.1
I2	5.0	3.8	4.1	4.1
I3	8.3	6.5	6.8	6.4
C	3.0	7.2	6.4	9.5
p1	6.5	5.7	6.6	7.0
P2	4.3	5.7	6.6	6.8
P3	4.2	5.0	7.0	6.2
P4	4.2	4.0	6.0	6.0
m1	6.0	5.2	5.5	7.0
m2	—	—	—	.5
Lower:				
I2	3.6	3.7	3.9	4.0
I3	4.8	3.8	4.5	4.2
C	2.0	7.4	7.0	9.0
p1	4.7	3.9	5.0	4.8
P2	5.9	4.0	5.5	5.0
P3	5.0	4.8	5.0	5.5
P4	3.3	3.0	3.7	4.3
m1	.6	.5	3.2	3.3
Total tooth heights	75.9	77.8	90.8	97.7
	Specimen data			
Age	92 days	66 days	83 days	73 days.
Date	Sept. 28	Sept. 2.	Sept. 19	Sept. 9.
Body lenght, cm	67	73	73	73.
Body weight, kg	8.4	6.8	8.0	8.5.
Percent MNW	175	142	167	177.

[1] Specimens are listed by increasing total tooth heights.
[2] A dash indicates an unerupted tooth.

Table 11.—*Gingival height of permanent teeth in the adult*

Teeth	Five males, age 10 years or older			Five females ages 6 to 15 years (mean 11)		
	Gingival height (mm)			Gingival height (mm)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Upper:						
I1	3.0	4.8	3.94	2.7	4.3	3.54
I2	3.7	6.0	5.18	2.8	4.8	3.96
I3	7.7	13.4	10.24	6.0	8.3	7.20
C	27.0	36.0	30.60	13.0	20.5	16.88
p1	6.2	7.2	6.66	4.4	8.2	6.68
P2	5.8	8.6	6.72	3.8	7.3	5.90
P3	4.1	7.1	5.66	4.0	6.9	5.58
P4	4.5	7.2	5.98	4.0	6.7	5.20
m1	4.0	10.5	6.58	2.0	[1] 6.5	4.45
m2	4.2	[1] 7.5	5.43	2.4	[1] 4.0	2.85
Lower:						
I2	.5	4.1	3.00	2.7	4.0	3.22
I3	1.0	6.7	4.64	3.0	4.8	4.06
C	22.0	27.0	25.00	9.0	17.3	13.94
p1	4.2	9.0	6.42	3.7	5.3	4.84
P2	5.0	7.8	6.14	4.5	6.1	5.42
P3	5.4	9.6	7.20	5.6	6.9	6.36
P4	4.9	9.0	7.02	4.9	6.7	6.04
m1	5.8	9.3	7.10	3.9	7.7	5.94

[1] Sample of four specimens only.

Table 12.—*Estimated sequence of gingival eruption of permanent teeth in the male*

Teeth	N [1]	Mean gingival height of tooth (mm)		Maturation percent [4]	Estimated sequence	
		In pups [2]	In adults [3]		A [5]	B [6]
Upper:						
I1	6	3.30	3.94	84	2	2
I2	6	3.43	5.18	66	4	4
I3	5	4.32	10.24	42	6	7
C	2	.58	30.60	2	16	16
p1	5	3.20	6.66	48	5	6
P2	5	1.33	6.72	20	9	9
P3	2	.78	5.66	14	11	12
P4	2	.45	5.98	7	14	14
m1	2	.67	6.58	10	12	13
m2	0	.00	5.43	0	18	18
Lower:						
I2	6	2.80	3.00	93	1	1
I3	6	3.82	4.64	82	3	3
C	2	.90	25.00	4	15	15
p1	6	2.65	6.42	41	7	5
P2	5	1.78	6.14	29	8	8
P3	5	1.32	7.20	18	10	10
P4	3	.58	7.02	8	13	11
m1	1	.03	7.10	1	17	17

[1] Number of specimens, out of six, in which the tooth has erupted.
[2] Mean gingival height of tooth in six pups (the first-listed in table 9).
[3] Mean gingival height of five adults (table 11).
[4] 100 (column 2/column 3).
[5] Sequence estimated from percent height only (see page 304).
[6] Sequence estimated from percent height and number of specimens in which the tooth has erupted.

It is clear that, within a tooth group, such as the upper incisors, eruption proceeds in an anteroposterior direction. It is not so clear, and is perhaps only a small-sample effect, that teeth in a mandibular group erupt earlier than those in the corresponding maxillary group. (It will be recalled that calcification is earlier in lower than in upper teeth.) The largest teeth, the canines, are 15th and 16th in order or eruption; only the osterior molars erupt later, 17th and 18th. For bout 6 weeks, while the permanent canines are rupting, the deciduous canines are functioning in heir stead.

At birth, in each upper quadrant, from 2 to 7 f the 10 permanent teeth may have cut the gum plate 4). Those which are consistently absent rom the oral cavities of five newborn specimens re P4, m1, and m2. In each lower quadrant, rom four to six of the eight permanent teeth ay have cut the gum. Only m1 is consistently bsent from the oral cavities of five newborn pecimens. Upper C has erupted in one out of ive specimens; lower C in two out of five. During brief perinatal period, the pup may have no osterior teeth at all, when the three deciduous olars above and below have exfoliated and only 1 above and below have cut the gums. During his period, the posterior one-third of each gum ne is dark pinkish gray, from congestion of lood at the sites of teeth about to erupt.

We conclude, from extrapolation of the evidence f tables 9 and 10, that the first permanent tooth lower I3) to erupt from the fetal gum does so in he fetus of 4.0 kg. (80 percent MNW, about 29 eeks implanted age), in early June, about 5 eeks before birth. The last tooth (upper m2) o erupt does so 6 to 13 weeks after birth, in ugust to October. It is nearly erupted in a pecimen of known-age 39 days; it is barely rupted in a specimen of 103 days. Permanent eeth in situ in the gums of a yearling are shown plate 12.

There is some evidence that supernumerary eeth are late in eruption. In the right upper uadrant of a pup several weeks old, an extra remolar is just cutting the gum between p1 and 2. The normal premolars are already in place, heir tips 3 mm. beyond the gum line.

An earlier statement by Scheffer (1950, p. 309) inexact. "When the fur seal is born in mid-ummer the canines, as well as most of the other ermanent teeth, have erupted." In fact, while e canines may have erupted, the well-formed d functional teeth which are usually visible in ch canine locus are the deciduous set. The ermanent canines cut the gum before age 10 eeks (tables 9 and 10, plate 13, A).

In the skulls of five males, age 10 years or older, e tips of the teeth are highest above the gum an adult, but not an old, individual, age 14 years (table 12). In the skulls of five females, ages 6 to 15 years, the teeth are highest in a 13-year-old (table 12).

Growth and Maturation of Permanent Teeth

Closure of the root.—As dentin is gradually deposited within the root canal of the permanent tooth, the diameter of the canal decreases. Eventually, the canal is filled and its blood vessels and nerves are pinched off (plate 13, B). The timing of root closure, by individual tooth and by sex, is shown in tables 13 and 14. Teeth such as lower

TABLE 13.—*Root closure in the permanent teeth, male*

Teeth	Age of specimen in months or years								
	9 mo.	14 mo.	14 mo.	2 yr.	2 yr.	3 yr.	3 yr.	4 yr.	4 yr.
	Stage of root closure [1]								
Upper:									
I1	—	o	—	x	x	x	x	x	x
I2	—	o	—	x	o	x	x	x	x
I3	closes in 7th to 10th year								
C	closes after 20th (?) year								
p1	—	—	—	—	—	—	—	o	—
P2	—	—	—	—	—	o	—	x	x
P3	—	—	—	—	—	x	—	x	x
P4	—	—	—	—	—	x	o	x	x
m1	—	—	—	x	o	x	x	x	x
m2	—	—	—	x	o	—	o	x	x
Lower:									
I2	—	x	x	x	x	x	x	x	x
I3	—	x	x	x	x	x	x	x	x
C	closes after 12th (?) year								
p1	—	—	—	x	o	x	o	x	x
P2	—	—	—	x	o	x	o	x	x
P3	—	—	—	o	—	x	o	x	x
P4	—	—	—	—	—	x	—	x	x
m1	—	—	—	o	—	x	o	x	x

[1] Symbols: Dash (—)=root canal open; o=root canal nearly closed; x=root canal closed.

TABLE 14.—*Root closure in the permanent teeth, female*

Teeth	Age of specimen in months or years					
	3 mo.	7 mo.	15 mo.	2 yr.	3 yr. [1]	3 yr. [2]
	Stage of root closure [3]					
Upper:						
I1	—	—	o	x	x	x
I2	—	—	o	x	x	x
I3	—	—	—	—	—	x
C	closes after 15th year					
p1	—	—	—	—	—	x
P2	—	—	—	—	—	x
P3	—	—	—	x	o	x
P4	—	—	—	o	o	x
m1	—	—	o	x	o	x
m2	—	—	—	—	o	x
Lower:						
I2	x	x	x	x	x	x
I3	o	o	x	x	x	x
C	closes in 7th or 8th year					
p1	—	—	—	o	o	x
P2	—	—	—	x	x	x
P3	—	—	—	—	o	x
P4	—	—	—	—	o	x
m1	—	—	—	—	o	x

[1] Slightly younger than 3 years on April 12.
[2] Slightly older than 3 years on September 11.
[3] Symbols: Dash (—)=root canal open; o=root canal nearly closed; x=root canal closed.

TABLE 15.—*Length of root of the permanent right upper canine with increasing age* [1]

Age	Males			Females		
	Length of root			Length of root		
	Number	Range	Mean	Number	Range	Mean
Years		*Mm.*	*Mm.*		*Mm.*	*Mm.*
0 [2]	4	0.3–0.7	0.5	--------	--------	--------
½ [3]	7	3.2–5.5	4.5	--------	--------	--------
1	2	9.1–9.2	9.1	3	--------	8.9
2	25	9.5–13.0	11.6	8	10.0–13.6	12.1
3	8	12.3–15.5	13.6	20	11.9–17.2	13.7
4	17	13.8–17.7	16.2	20	12.2–17.0	14.7
5	2	17.0–17.1	17.1	20	13.7–18.0	14.9
6	1	--------	21.8	20	13.7–20.6	16.7
7	2	22.3–24.1	23.2	20	16.5–20.2	18.5
8	1	--------	33.1	18	15.6–20.9	18.3
9	--------	--------	--------	5	15.7–19.8	18.3
10	3	28.4–33.2	30.3	21	17.6–23.9	19.8
11	--------	--------	--------	13	18.9–23.4	20.3
12	--------	--------	--------	2	17.0–23.0	19.6
Old [4]	--------	--------	--------	9	19.1–24.3	21.6

[1] Unless otherwise noted, data are from known-age (marked) seals recovered on the Pribilof Islands in summer.

[2] Full-term fetal, July 6, 1957.

[3] "Yearlings" about 6 to 7 months old, found dead or dying on Oregon beaches after a storm, late January to early February 1950.

[4] Nine canines with crown worn and root canal closed, or nearly closed, selected from 100 unmarked females killed on a breeding ground, October 3, 1950.

incisors, with slender roots, close earlier than teeth, such as canines, with larger roots.

Evidence on the maximum age of root closure in male teeth is poor (table 13). The oldest known-age skull in the collection is a 14-year-old. In three 10-year-olds, the diameter of the right upper canine root canal is 6, 8, and 8 mm., respectively—far from closed. In an 11-year-old, it is 8 mm., while the diameter of the lower canine canal is 0.3 mm. In the 14-year-old it is 7 mm., and the canals of the lower canines are closed. In a very old individual of undetermined age, with worn and polished teeth, the root of the left upper canine still has a canal 0.6 mm. in diameter, whereas the root of the left lower canine has long since closed. We tentatively conclude that upper canines in the male close after the 20th year (or in some individuals never?); lower canines after the 12th.

Evidence on the maximum age of root closure in female teeth is more conclusive (table 14). In the upper canines of 44 females (23 ten-year-olds, 15 eleven-year-olds, 4 twelve-year-olds, and 2 fifteen-year-olds), the diameter of the root canal varies from 0.1 to 1.5 mm., average about 0.5 mm. In the two 15-year-olds, the diameter of the canal is 0.2 mm. In a 21-year-old, the canal is closed. We conclude that the female upper canine closes after the 15th year.

Growth of the root.—Increase in size of the growing root has been studied for the right upper canine. This tooth was selected in 1949 as the one which would be used, in future Pribilof seal studies, as an indication of age. Length of root by age and sex is given in table 15. Changes in the root are illustrated in plates 14 and 15. At birth, when the upper canine is largely hidden within the bony alveolus, the root is less than 1 mm. in length. On the evidence of its size and shape, the root grows rather uniformly during the 3- to 4-month period when the pup is nursing. At time of weaning, when the pup learns to feed for itself, growth of the root declines. The evidence is a faint "first-autumn depression" or valley circling the root. Some teeth show it plainly (plate 15), others do not. At completion of the first year of life, a "second-autumn depression" is formed around the root. Another depression is formed in the third autumn, and in each successive autumn until the seal approaches an age of 10 to 15 years. Then each depression tends to become shallow and narrow and to be hidden by a deposit of cementum (plate 16).

As long as the root canal remains open, dentin is deposited on the walls of the root cavity, the deposit being thicker and more opaque in winter, spring, and summer; thinner and more translucent in fall. As a result of this unequal deposition, each annual layer is visible on a longitudinally sectioned tooth as a discrete cone slightly smaller than, and nesting within, the cone of the previous year (plate 17). Meanwhile, a thin but fairly distinct layer of cementum is being laid down annually on the outside of the root. The source of the cementum is the connective tissue surrounding the root, not the pulp of the tooth. Cementum layers continue to be laid down after the root canal closes. Zander and Hürzeler (1958) measured cementum thickness on 233 single-rooted human teeth and found that it showed a straightline increase with age. Thickness tripled between ages 11 and 76 years. This was "surprising in view of the fact that growth processes usually decrease with advancing age" (p. 1043).

Kubota et al. (1961) described growth layers near the level of the cementoenamel junction. These are, from outside inward: cementum, prenatal dentin (opaque), neonatal line (translucent), postnatal dentin consisting of (a) interglobular dentin mixed with the granular layer of Tomes and (b) a translucent layer which is formed in spring. When the root canal closes, dentin ceases to orm in regular conical layers. While stratified eposits of some tooth substance continue to form t the base of the root, they tend to be thin and rregular, and we do not know what to call them. Ve sliced longitudinally and polished all of the ight teeth of a known-age 13-year-old female. The smallest tooth, the 1st lower incisor, whose oot canal probably closed within the 1st year of ife, shows no distinct layers in the dentin. The ower canine, where the root canal probably losed in the 7th or 8th year, shows seven conical ayers of dentin. The upper canine, where the oot canal is still open, shows 13 layers.

Annual growth lines in the teeth of the seal evelop in both sexes, and in captive as well as vild individuals. Growth of the root is always lower in autumn. We suggest that the period of low growth is related to the annual molt of the elage which takes place in autumn in seals of all lasses (Scheffer, 1962). A male seal was captured n the Pribilof Islands on October 17, 1948 and vas delivered to the San Diego Zoo a few days ater. It died on May 18, 1953, after almost 5 ears in captivity. The root of its right upper anine is of normal size (length 22.6 mm.); the rowth ridges are somewhat confused (plate 18). evertheless, two experienced biologists (C. E. begglen and A. Y. Roppel) estimated correctly nd independently the age of the seal as 5 years. ansfield and Fisher (1960) counted 18 to 20 ayers on the tooth of a harbor seal *Phoca* that ad been brought as a pup to the Seattle Zoo and ied there at age 19½ years.

The relative importance of the various environ-ental factors which contribute to the formation f growth ridges cannot now be evaluated. It eems possible both that molt in autumn may ause a decrease in deposition of root substance nd that heavy feeding in spring may cause an ncrease. There is ancillary evidence that most f the annual body weight increment is added in pring.

From the evidence of certain teeth (plate 9, B and C), the accretion of root substance may uddenly accelerate or decelerate. Ridges on he surface of the growing root, finer than annuli nd spaced between them, are thought to originate n individual periods of intensive feeding. Plate 9, A reproduces a gelatin impression of the surface f a yearling male canine tooth. The seal was illed on September 13, at estimated age 14 months. Around the root one can count about 25 fine ridges, more or less distinct, arranged in a near-rhythmic pattern.

Typical postcanine roots in situ in a middle-aged seal are illustrated in plate 8. Other roots, somewhat atypical as a result of bone resorption, are shown in plate 20, A.

Crown.—The crowns of the permanent teeth become streaked and stained dark brown soon after birth. In a specimen a few days old taken on June 26, (female, 4.4 kg., 92 percent MNW) the teeth are already moderately stained. The pigment is heaviest on the posterior series of teeth and on buccal, as opposed to lingual, surfaces. The chemistry of the pigment is not known.

Tooth crowns of the fur seal do not suffer wear to the same extent as do crowns of land carnivores like wolf and bear. Where the dentin of the seal tooth has been exposed, its surface becomes polished and shiny (plate 20, B).

For each canine showing crown-tip wear, we have estimated its height, had there been no wear (tables 7 and 8). Tip wear is insignificant in 1-, 2-, and 3-year-olds. On the upper canines of 6- and 7-year-olds, it may reach 1 mm. in males and 0.7 in females; on the lower canines, a little less.

GROWTH CHANGES IN SKULL AND JAWS

In both sexes, the halves of the mandible remain separate through life, as in the dog but not in man. They are united by tough connective tissue and cannot easily be pulled apart. Right and left molariform tooth rows are nearly parallel. They may diverge posteriorly up to 5 degrees. Each approaches a straight line, though it may be slightly convex or, rarely, concave. The shape of the tooth row does not vary appreciably with age or sex (plates 21 and 22).

A useful indication of physiological age or maturity of the individual is the size of the skull. We have measured condylobasal length and cranial width for 76 skulls (34 males and 42 females), and have compared them with measurements of the upper and lower postcanine series (tables 16 and 17 and figures 3 and 4). The results are summarized on page 310.

Male

Condylobasal lengths in two newborn males are 121 and 122 mm.; in three old adults they are

TABLE 16.—*Skull size and length of the permanent postcanine series, by age, male*

Age	Specimens	Condylobasal length	Cranial width	Length of postcanine series	
				Upper	Lower
	Number	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Percent MNW [1]					
25	1	72	55	19	21
33	1	81	58	20	18
33	1	85	61	20	20
42	1	90	67	22	21
Newborn	2	121	85	33	29
Weeks, 1–2	1	129	86	33	32
Ca. 9 months	1	143	91	35	30
Ca. 14 months	2	165	95	[2] 39	35
Years:					
2	2	173	93	40	33
3	3	180	98	43	36
4	2	191	95	44	36
5	3	200	102	47	38
6	2	213	107	49	40
7	2	213	106	[3] 45	38
8	[4] 3	241	133	[2] 53	43
9	1	232	126	[2] 52	43
10	3	230	122	50	41
10+	3	241	132	54	43
Total	34				

[1] Fetus, 25 percent of mean newborn weight.
[2] One skull has an extra pair of upper premolars.
[3] One skull lacks a pair of upper premolars.
[4] For one broken skull, measurements of skull size are lacking.

TABLE 17.—*Skull size and length of the permanent postcanine series, by age, female*

Age	Specimens	Condylobasal length	Cranial width	Length of postcanine series	
				Upper	Lower
	Number	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Percent MNW [1]					
28	1	79	59	21	19
33	1	84	64	21	20
38	1	85	63	21	22
56	1	99	76	24	22
Newborn	2	122	84	33	27
Ca. 3 months	1			33	29
Ca. 7 months	1	140	88	33	28
Ca. 8 months	1	145	89	35	31
Ca. 15 months	2	159	95	38	35
Years:					
2	3	163	93	40	32
3	2	173	94	39	32
4	4	172	93	42	33
5	7	174	91	41	34
6	2	185	93	48	37
7	2	183	98	44	37
8	2	180	92	43	33
9	3	183	95	44	35
10	1	180	91	42	33
10+	5	190	96	46	36
Total	42				

[1] Fetus, 28 percent of mean newborn weight.

237, 242, and 243 mm. The difference represents a mean increase through life of 98 percent over newborn size. Cranial widths in two newborn males are 85 and 86 mm.; in three old adults they are 131, 131, and 135 mm. The difference represents a mean increase through life of 55 percent. The skull of a male at age 8 or 9 is about as large as it ever will be, though length and width increase slightly after age 9 as a result of bony growth of the premaxillary and mastoid processes.

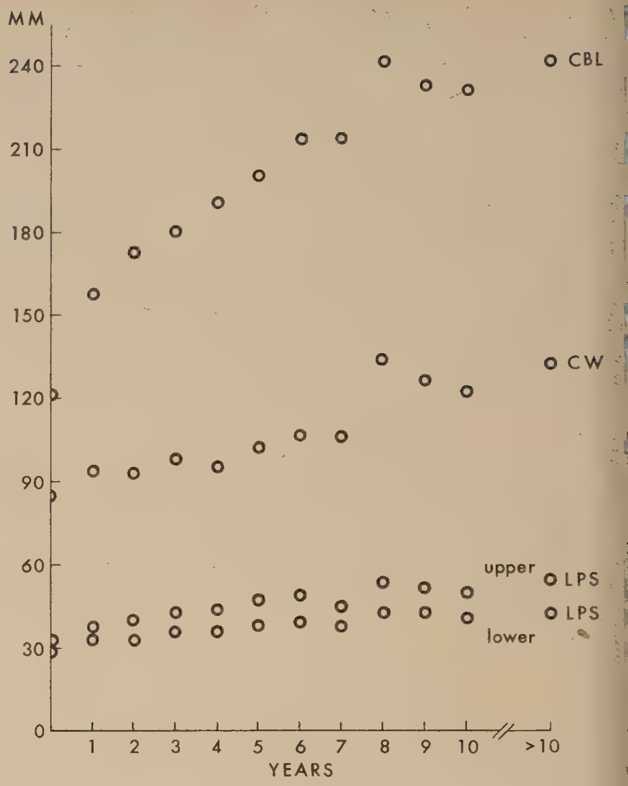


FIGURE 3.—Condylobasal length, cranial width, and length of permanent postcanine series, by age, male. (From table 16, based on 30 specimens.)

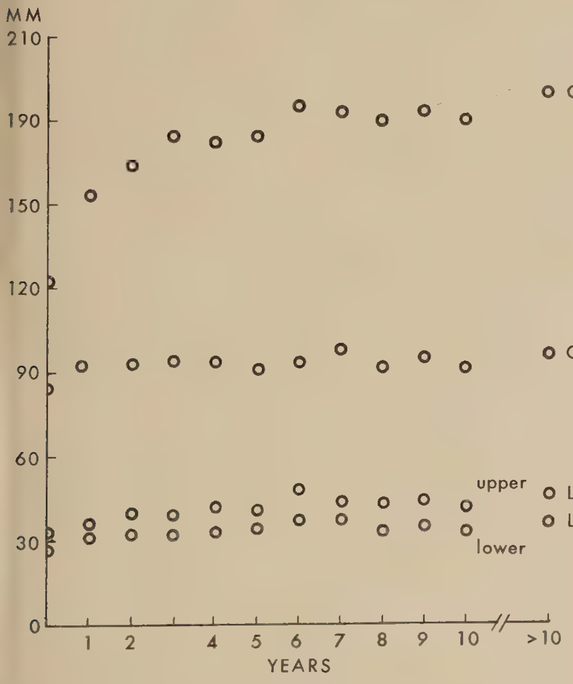
In estimating the age at which skull growth reaches a plateau, we have also referred to published data on condylobasal length and mastoid width of 108 fur seal skulls (Scheffer and Wilke, 1953).

Lengths of upper postcanine series in two newborn males are 32 and 33 mm.; in three old adults, 53, 55, and 55 mm. The difference represents a mean increase of 67 percent. The upper jaw does not increase in length after age 8 or 9.

Lengths of lower postcanine series in two newborn males are 29 and 29 mm.; in two old adults, 43 and 43 mm. The difference represents a mean increase of 48 percent. The lower jaw does not increase in length after age 8 or 9. Growth changes in the lower jaw of the male are illustrated in plate 23. In the sample illustrated, the length of the jaw increased by 54 percent in the period from birth to age 3 (the age of sexual maturity in some males). It increased 53 percent between age 3 and adulthood. This growth spurt in postpubertal life, observed in the male nly, is related to the fact that the fur seal is olygynous. To the adult male attempting to old his place in a fiercely competitive social rder, strong jaws and teeth have survival value. n the same sample, the ratio of length of jaw o length of postcanine series is 2.4:1 for the ull-term fetus and 3.9:1 for the old adult. The ostcanine tooth-row grows slower than the nandibular corpus posterior to it. The postcanine ooth-row itself increased 45 percent (29 to 42 nm.). As the tooth row lengthens, the diameter f each socket increases; the spatial arrangement f the tooth row remains fairly constant.

emale

Condylobasal lengths in two newborn females re 121 and 123 mm.; in five old adults they are 85, 189, 191, 191, and 196 mm. The difference epresents a mean increase through life of 56 ercent. Cranial widths in two newborn females re 82 and 96 mm.; in five old adults they are 95, 6, 96, 96, and 99 mm. The difference represents mean increase through life of 15 percent. The kull of the female does not appear to grow in ength or width after age 5 or 6. With respect to kull size, the female reaches maturity about 3 ears before the male.



IGURE 4.—Condylobasal length, cranial width, and length of permanent postcanine series, by age, female. (From table 17, based on 38 specimens.)

Length of upper postcanine series in two newborn females are 32 and 33 mm.; in five old adults 45, 45, 46, 46, and 49 mm. The difference represents a mean increase of 42 percent. The upper jaw continues to grow in length until age 5 or 6.

Lengths of lower postcanine series in two newborn females are 26 and 28 mm.; in five old adults 34, 35, 36, 37, and 37 mm. The difference represents a mean increase of 33 percent. The lower jaw continues to increase in length until age 5 or 6.

ANOMALIES

Prenatal

In a sample of 123 skulls of both sexes, 14 (or 11 percent) show anomalies of the dentition. Four have extra teeth. Ten lack one or two teeth, and apparently did not have them at time of birth.

Of the four skulls with extra teeth, three have extra premolars in the upper middle series and one has extra premolars in the lower middle series (plate 24). The skull with extra lower premolars is remarkable for having 45 teeth—9 extra! It has three extra upper incisors lingual to, and similar to, I1 and 2; four extra lower incisors lingual to I2 and 3; and a pair of extra lower premolars between P2 and 3.

In the dog, when supernumerary teeth are present, they are incisors or premolars, usually unilateral and in the upper jaw (Miller, 1952). In the fur seal (as noted in three out of four cases), extra premolars in the upper jaw are more common than in the lower.

Of the 10 skulls with teeth prenatally lost, 4 lack one and 6 lack both upper m2. This posterior tooth, which is unopposed, is small and weak. It quite certainly has the least function of any of the teeth. Where there is unilateral absence, the remaining one may be unusually small, or be broken off at the alveolar rim. We suspect that m2 can be lost in early postnatal life when the maxillary bone is still growing actively and is able to fill in the bony alveolus without trace. Thus, one cannot always distinguish, in an adult skull, between prenatal and postnatal loss of m2. According to Simpson (1961, p. 100) "a tooth . . . that no longer occludes or that is in the process of reduction and loss of essential function (like the human wisdom teeth) is demonstrably exceptionally variable in both structure and size."

In addition to the random sample of 123 skulls utilized in this report, 4 selected "freaks" were

TABLE 18.—*Beginning events in the dental development to age 12 weeks* [1]

Body weight	Approximate percent mean newborn weight	Approximate month	Deciduous teeth					Permanent teeth			
Kg											
0.05	1	December	------	------	------	------	------	------	------	------	------
.10	2	January	*CC*	------	------	------	------	------	------	------	------
.15	3	January	*CC*	------	------	------	------	*CC*	------	------	------
.20	4	January	------	*AE*	------	------	------	*CC*	------	------	------
.25	5	January	------	*AE*	------	------	------	*CC*	------	------	------
.30	6	February	------	*AE*	------	------	------	*CC*	------	------	------
.35	7	February	------	*AE*	------	------	------	*CC*	------	------	------
.40	8	February	------	*AE*	------	------	------	*CC*	------	------	------
.45	9	February	------	------	------	------	------	*CC*	------	------	------
.5	10	February	------	------	------	------	------	*CC*	------	------	------
1.0	20	March	------	------	------	*RC*	------	*CC*	------	------	------
1.5	30	March	------	------	*GE*	*RC*	------	*CC*	------	------	------
2.0	40	April	------	------	*GE*	*RC*	------	*CC*	------	------	------
2.5	50	April	------	------	*GE*	*RC*	*EX*	*CC*	*AE*	------	------
3.0	60	May	------	------	*GE*	*RC*	*EX*	*CC*	*AE*	------	------
3.5	70	May	------	------	------	*RC*	*EX*	*CC*	*AE*	------	------
4.0	80	June	------	------	------	*RC*	*EX*	------	*AE*	*GE*	------
4.5	90	June	------	------	------	*RC*	*EX*	------	*AE*	*GE*	------
5.0	100	July (birth)	------	------	------	*RC*	*EX*	------	*AE*	*GE*	------
8.0	160	August (age 6 weeks)	------	------	------	------	*EX*	------	------	*GE*	------
13.0	260	October (age 12 weeks)	------	------	------	------	------	------	------	------	*RC*

[1] These events are beginning in one or more teeth: *CC*=crown calcification, *AE*=alveolar eruption, *GE*=gingival eruption, *RC*=root closure, and *EX*=exfoliation.

observed: (1) a skull with an extra pair of upper premolars between P2 and 3, (2) a skull with supernumerary upper canines, (3) a skull with seven extra teeth in the upper and lower series of incisors and anterior premolars, and (4) a skull with an extra pair of lower molars. The last was figured by Scheffer (1958). It is remarkable in that it represents the only known specimen having an extra tooth at the posterior end of a tooth row.

Postnatal

Damage represented by empty sockets, or teeth broken off, is apparent in both sexes and in both upper and lower jaws. In the lower jaw of a 7-year-old female, P3 is deformed and blackened (plate 25, A). Evidently the crown was accidentally broken; then an abscess formed around the root and the bone of the socket eroded. In a young male, about 6 years old, that died in the Seattle Zoo, right upper C is greatly deformed (plate 25, B). Here also a root abscess is the cause. From the left mandible of an old female, the four premolars have been lost and the bone itself has undergone extensive change (plate 26, A). The bony alveoli of a male raised in captivity have a spongy, eroded appearance (plate 26, B).

We have seen no evidence of caries in seal teeth. Hall (1940) examined the skulls of 3,761 land carnivores and found caries in 2 percent of 360 bears (*Ursus* and *Euarctos*), but in no other carnivores.

SUMMARY AND CONCLUSIONS

The dentitions of 167 specimens of *Callorhinus ursinus* ranging from early fetal life to adulthood have been studied. Crown and root morphology of deciduous and permanent teeth are described. A terminology is presented for the kinds of teeth, their topographic relationships, their developmental stages, and their measurements. The time sequence is shown for calcification, alveolar eruption, gingival eruption, root closure, and exfoliation (table 18). Formulas are presented for deciduous, mixed, and permanent dentitions (fig. 5). Increase with age is shown for skull length and width, and for length of upper and lower postcanine series. Certain prenatal and postnatal anomalies, especially supernumerary and absent teeth, are described. The following observations and conclusions are believed to be new or worthy of emphasis:

1. Calcification is initiated in all deciduous teeth between implanted ages 7 and 9 weeks, when the fetus has attained 2 or 3 percent of its estimated newborn weight. Initial calcification in the permanent teeth overlaps that in the deciduous teeth, though it is still in progress up to about implanted age 27 weeks and 70 percent estimated newborn weight. The very early development of the permanent teeth enables the young seal, at age 3 or 4 months, to convert abruptly from a diet of milk to one of fish and squid.

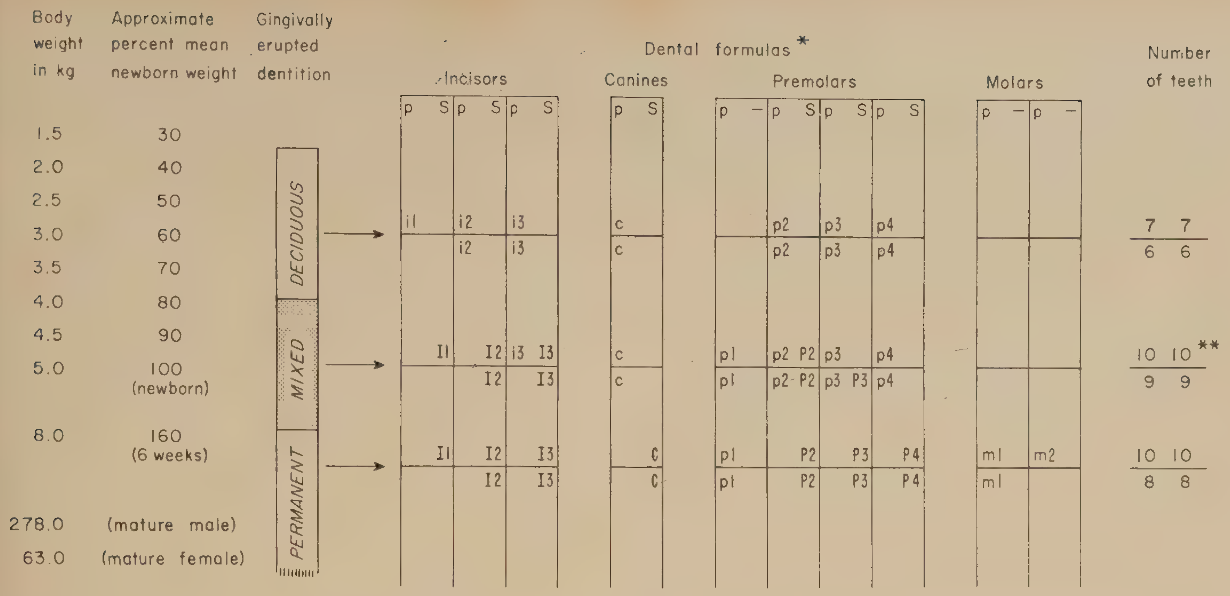

Body weight in kg
Approximate percent mean newborn weight
Gingivally erupted dentition
Dental formulas *
Incisors
Canines
Premolars
Molars
Number of teeth
1.5 30
2.0 40
2.5 50
3.0 60
3.5 70
4.0 80
4.5 90
5.0 100 (newborn)
8.0 160 (6 weeks)
278.0 (mature male)
63.0 (mature female)
DECIDUOUS
MIXED
PERMANENT
p S p S p S
p S
p – p S p S p S
p – p –
i1 i2 i3 c p2 p3 p4 7 7
i2 i3 c p2 p3 p4 6 6
I1 I2 i3 I3 c p1 p2 P2 p3 p4 10 10 **
I2 I3 c p1 p2 P2 p3 P3 p4 9 9
I1 I2 I3 C p1 P2 P3 P4 m1 m2 10 10
I2 I3 C p1 P2 P3 P4 m1 8 8

FIGURE 5.—Dental formulas at three stages of development.

*Primary teeth are in small letters; secondary teeth in large. Maxillary teeth are shown above the bar, mandibular teeth below.

**The mixed (successional) dentition is highly variable. Shown here are teeth which have usually erupted in the perinatal period.

2. With the exception of the canines, the deciduous teeth are nonfunctional. The smaller ones (incisors) exfoliate during fetal life; the premolars exfoliate during perinatal life; one or another of the canines may persist for 13 weeks after birth. With the exception of the canines, which cut the gums early, the sequence of gingival eruption is random, or nondirectional, in the tooth rows.

3. At birth, the crown tips of all of the permanent teeth are at, or above, the bony alveolar rims. From two to seven teeth in each upper quadrant, and from four to six in each lower quadrant, may have cut the gums. Variability in the neonatal (mixed) dentition has apparently little significance for survival. The last permanent tooth (upper m2) erupts at age 6 to 13 weeks. Directionally, the sequence of gingival eruption is anterior to posterior, except in the canines.

4. If a "lower 1st incisor" was present in ancestral seals, it has left no embryological trace. In each upper quadrant the 1st premolar (1st postcanine) and the 1st and 2d molars (5th and 6th postcanines) are, on embryological evidence, primary permanent teeth. Similarly, in each lower quadrant the 1st premolar and the 1st molar are primary permanent teeth.

5. The lower medial incisors (I2) and the upper and lower premolars (P2, P3, and P4) usually have anterior and posterior cusplets, suggesting an origin in distinctly tricuspid, perhaps triconodont, teeth. Upper m2 is nearly always double-rooted; certain other posterior teeth are occasionally so. The percentage of consistently double-rooted teeth in the deciduous dentition is 23.1; in the permanent dentition 5.5, suggesting that there has been an evolutionary trend toward a single root.

6. The roots of the permanent teeth continue to grow through life, more slowly after the root canal closes. It closes at age 3 months in small teeth, and at some time after 20 years in large teeth. Annual discontinuities (ridges and layers) occur outside and inside the root; up to 27 have been counted.

7. Skull size and length of postcanine series increase very little after age 8 or 9 years in the male and age 5 or 6 years in the female.

8. In a sample of 123 skulls, the dentitions of 14 (or 11 percent) are anomalous. Four have supernumerary teeth and ten have prenatally absent teeth. Supernumerary teeth have been found in the molar series only once: in lower m1 locus. Upper m2 has no antagonist and, when present, is quite variable in size.

9. Among the problems remaining unsolved are the sequence of calcification of the upper deciduous teeth and the mechanism of gingival eruption of

the deciduous teeth. The frequency distribution of deciduous and permanent teeth in the neonatal (mixed) dentition is known to be highly variable. A more precise understanding of the variability could be obtained by collecting more specimens of newborn pups.

LITERATURE CITED

Allen, Glover M.

1880. History of North American pinnipeds, a monograph of the walruses, sea-lions, sea-bears, and seals of North America. United States Geological and Geographical Survey of the Territories, Miscellaneous Publications 12, 16+785 pp.

Allen, Joel Asaph, and Charles Bryant.

1870. On the eared seals (Otariadae), with detailed descriptions of the North Pacific species . . . Bulletin of the Museum of Comparative Zoology, Harvard, vol, 2, pp. 1–108, 3 pls.

Bartholomew, George A., Jr., and Paul G. Hoel.

1953. Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. Journal of Mammalogy, vol. 34, No. 4, pp. 417–436.

Bokstrom, Peter.

1961. A study of the maxillary permanent dentition of the Alaskan fur seal during fetal life. Seattle, University of Washington, Thesis, Master of Science in Dentistry, 55 typewritten pages.

Chiasson, Robert B.

1955. Dental abnormalities of the Alaskan fur seal. Journal of Mammalogy, vol. 36, pp. 562–564.

1957. The dentition of the Alaskan fur seal. Journal of Mammalogy, vol. 38, pp. 310–319.

Frechkop, Serge.

1955. [Teeth of pinnipeds, Tome 17, Fascicle 1, p. 299–300.] *In* Traité de zoologie . . . publié sur la direction de Pierre -P. Grassé. Masson, Paris, 18 vols.

Grassé, Pierre -P.

1955. [Teeth of carnivores, Tome 17, Fascicle 1, p. 205–207.] *In* Traité de zoologie . . . publié sur la direction de Pierre -P. Grassé. Masson, Paris, 18 vols.

Gregory, William King.

1951. Evolution emerging. Macmillan, New York, 2 vols.

Hall, E. Raymond.

1940. Supernumerary and missing teeth in wild mammals of the orders Insectivora and Carnivora, with some notes on disease. Journal of Dental Research, vol. 19, pp. 103–143 (including 12 pls.).

Howell, A. Brazier.

1929. Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). Proceedings of the U.S. National Museum, vol. 73, pp. 1–142, 1 pl.

Kellogg, Remington.

1922. Pinnipeds from Miocene and Pleistocene deposits of California . . . and a résumé of current theories regarding origin of Pinnipedia. Bulletin of the Department of Geology, University of California, vol. 13, pp. 23–132.

Kraus, Bertram S.

1959. Calcification of the human deciduous teeth. Journal of American Dental Association, vol. 59, pp. 1128–1136.

Kubota, Kinziro, Hiroshi Komuro, Fukuzo Nagasaki, Morio Tsuboi, and Koji Matsumoto.

1961a. The eruption and shedding of teeth in the fur seal. Okajimas Folia Anatomica Japonica, Band 37, Heft 4–5, pp. 331–337. (English)

1961b. The calcification of teeth of the fur seals (roentgenographic examination). Okajimas Folia Anatomica Japonica, Band 37, Heft 6, pp. 389–419. (English)

Kubota, Kinziro, Fukuzo Nagasaki, Koji Matsumoto, and Morio Tsuboi.

1961. Histological studies on the growth layers in the maxillary canines of fur seals as an indicator of age. Part 1. The teeth at the age of one to nine year. Bulletin, Tokyo Medical and Dental University, vol. 8, No. 3, pp. 261–285. (English)

Kükenthal, Willy.

1894. Entwickelungsgeschichtliche Untersuchungen am Pinnipediergebisse. Jenaische Zeitschrift f. Naturwissenschaft, Band 28 (Neue Folge, Band 21), pp. 76–118, 2 pls.

Lamb, Mardon C.

1962. Observations on the embryonic development of the mandibular dentition in the Alaska fur seal. Thesis, Master of Science in Dentistry, University of Washington, Seattle, 4+57 pp. processed.

Laws, R. M.

1962. Age determination of pinnipeds with special reference to growth layers in teeth. Zeitschrift für Säugetierkunde, Band 27, Heft 3, pp. 129–146.

Lucas, Frederic A.

1899. The dentition of the fur seal [part 3, pp. 9–11, pls. 1–2]. *In* The fur seals and fur-seal islands of the north Pacific Ocean . . . by Jordan *et al.* U.S. Treasury Department, Document 2017, 4 parts.

Mansfield, A. W., and H. D. Fisher.

1960. Age determination in the harbour seal, *Phoca vitulina* L. Nature, vol. 186, pp. 92–93.

Miller, Malcolm E.

1952. Teeth [pp. 32–35]. *In* Guide to the dissection of the dog. 3d edition, reprinted. Published by author, Ithaca, New York, 427 pp.

Osborn, Henry Fairfield.

1907. Pinnipedia [pp. 143–144]. *In* Evolution of mammalian molar teeth. . . . Edited by W. K. Gregory. Macmillan, New York, 10+250 pp.

earson, Anita K., and Robert K. Enders.
1951. Further observations on the reproduction of the Alaskan fur seal. Anatomical Record, vol. 111, No. 4, pp. 695–711.

and, Robert W.
1950. On the milk dentition of the Cape fur seal. Journal of the Dental Association of South Africa, vol. 5, pp. 462–471.

cheffer, Victor B.
1950. Growth layers on the teeth of Pinnipedia as an indication of age. Science, vol. 112, pp. 309–311.
1958. Seals, sea lions, and walruses; a review of the Pinnipedia. Stanford University Press, 10+179 pp., 32 pls.
1960. Early embryos of the northern fur seal. Mammalia, Tome 24, No. 3, pp. 482–483, 1 pl.
1962. Pelage and surface topography of the northern fur seal. U.S. Fish and Wildlife Service, North American Fauna 64, 6+206 pp.

cheffer, Victor B., and Ford Wilke.
1953. Relative growth in the northern fur seal. Growth, vol. 17, pp. 129–145.

ergeant, D. E.
1959. Age determination in odontocete whales from dentinal growth layers. Norsk Hvalfangst-Tidende (Norwegian Whaling Gazette), vol. 48, pp. 273–288, illus., June.

Simpson, George Gaylord.
1945. The principles of classification and a classification of mammals. American Museum Natural History, Bulletin 85, 16+350 pp.
1961. Principles of animal taxonomy. Columbia University Press, New York, 14+247 pp.

Swindler, D. R., and J. A. Gavan.
1962. Calcification of the mandibular molars in rhesus monkeys. Archives of Oral Biology, vol. 7, pp. 727–734.

Takano, James H.
1961. A study of the mandibular dentition of the Alaska fur seal fetus. Seattle, University of Washington, Thesis, Master of Science in Dentistry, 56 typewritten pp.

Todd, T. Wingate.
1918. Pinnipedia [p. 185-187]. *In* An introduction to the mammalian dentition. Henry Kimpton, London, 290 pp.

Weber, Max.
1928. Carnivora Pinnipedia [Band 2, pp. 342–354]. *In* Die Säugetiere . . . with collaboration of Othenio Abel. Gustav Fischer, Jena, 1927–28, 2 vols.

Zander, H. A., and Beat Hürzeler.
1958. Continuous cementum apposition. Journal of Dental Research, vol. 37, pp. 1035–1044.

PLATES

The numbers in parentheses following a caption are photo-catalog numbers in the VBS series, the Marine Mammal Biological Laboratory.

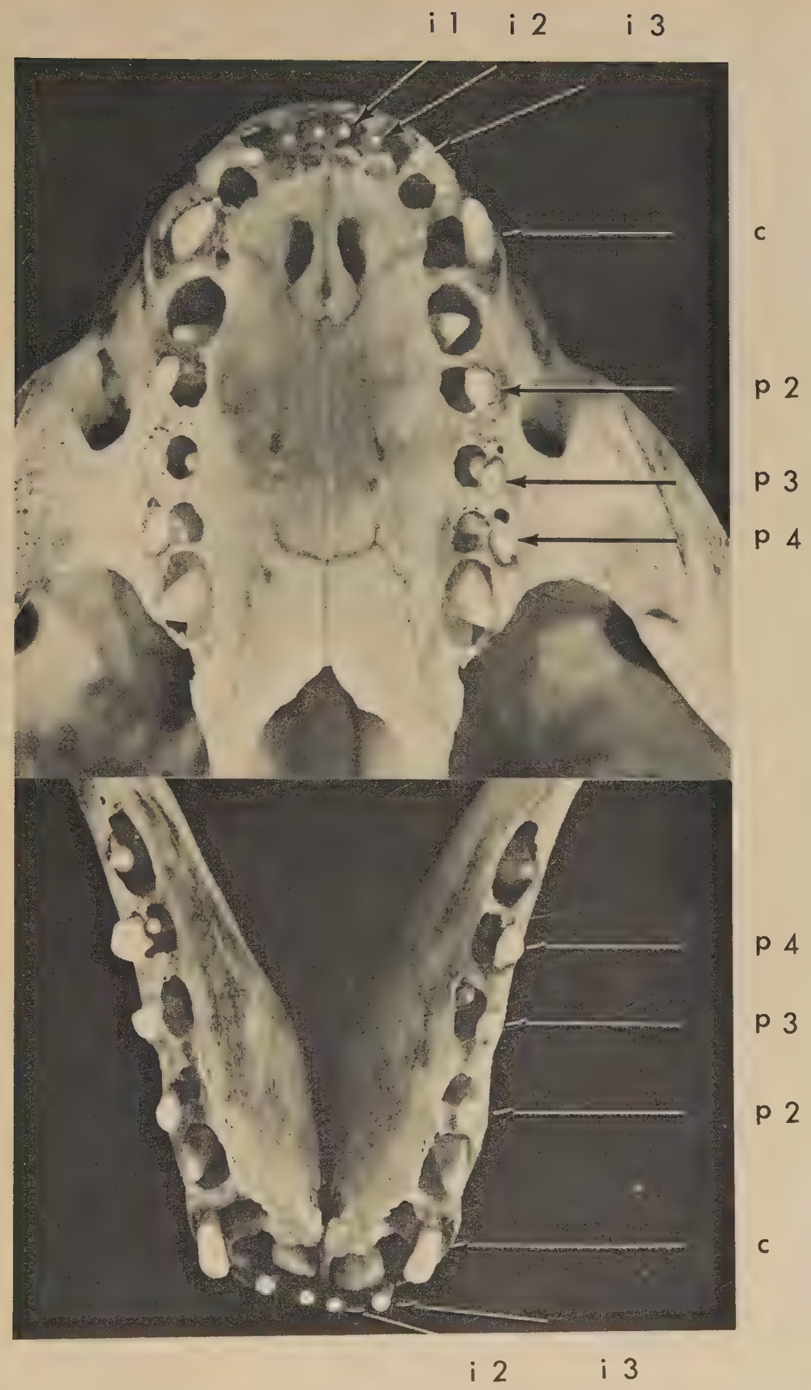

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PLATE 1.—Complete deciduous dentition of a fetal female of 1.59 kg., 33 percent MNW. (For terminology of teeth see p. 296.) (4348, 4349)

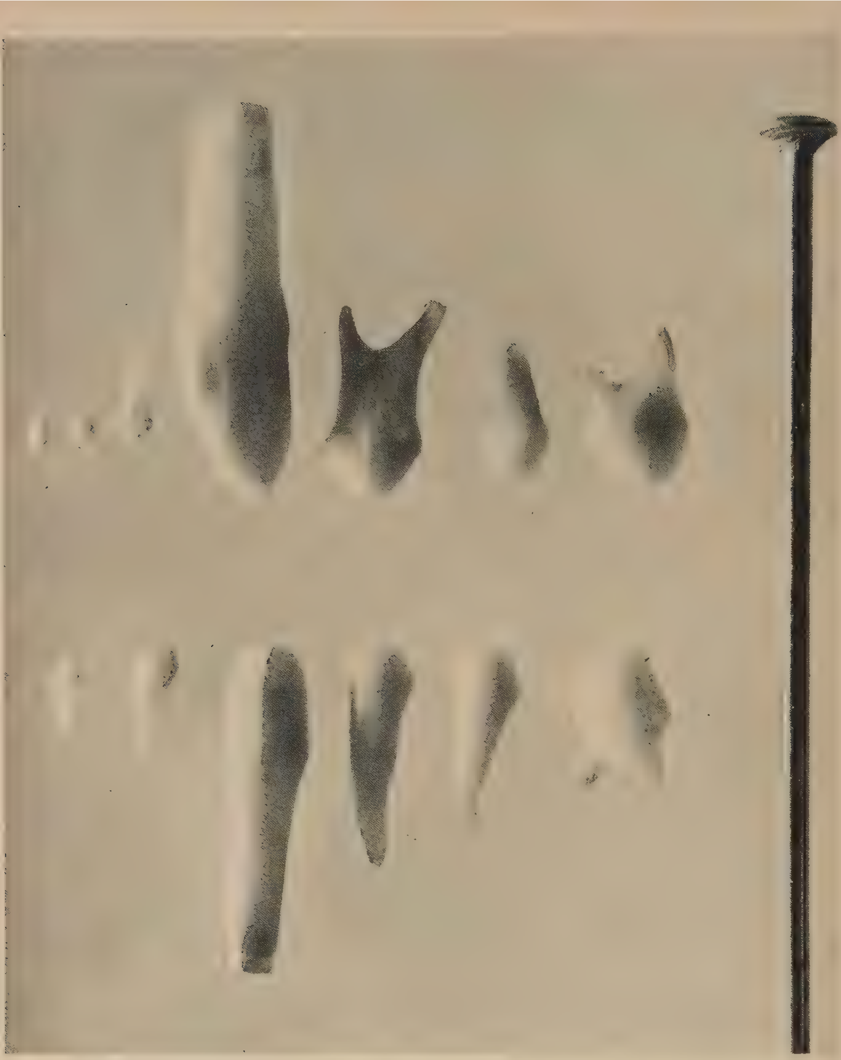

Plate 2.—Deciduous teeth of the fetal female illustrated in plate 1; left teeth, labial or buccal surfaces; common pin at right. (4385)

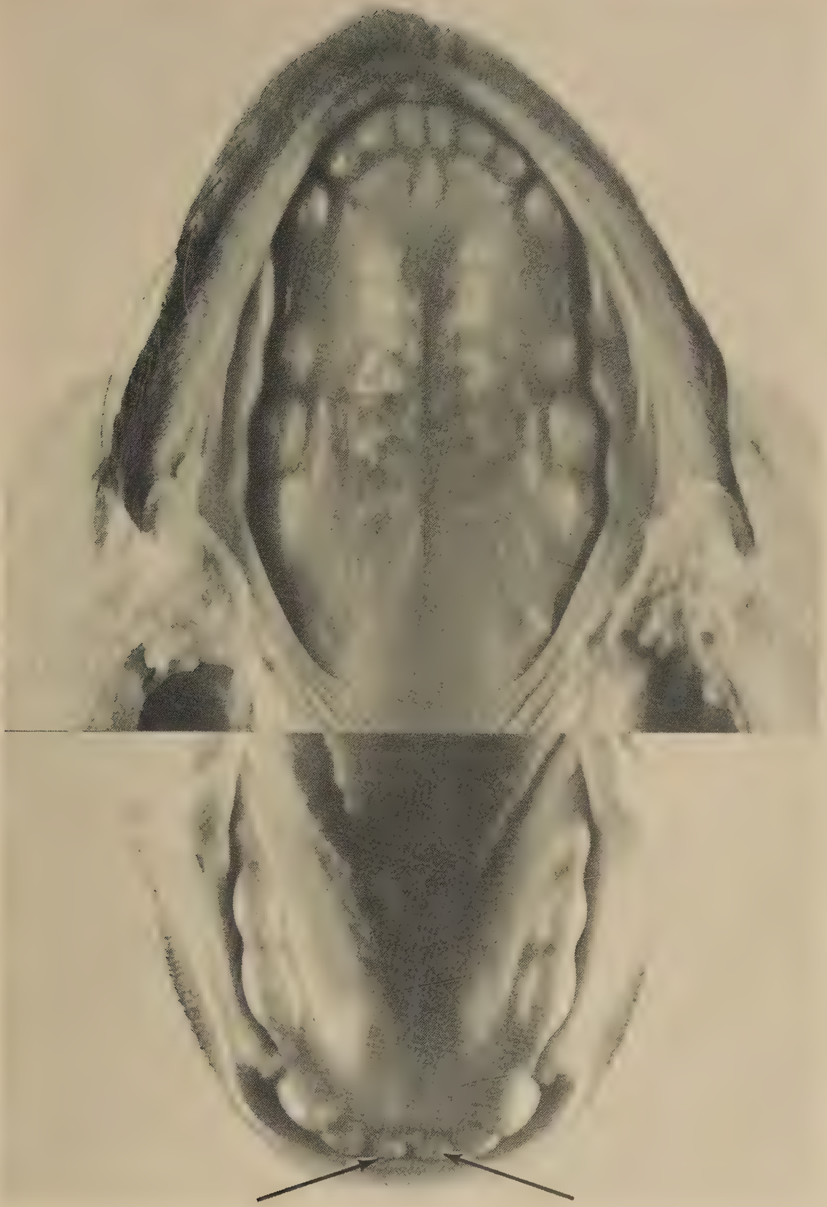

PLATE 3.—Deciduous dentition of a fetal female of 1.70 kg., 34 percent MNW, at onset of gingival eruption. Only lower right and left i2 (arrows) have started to erupt. (4388, 4389)

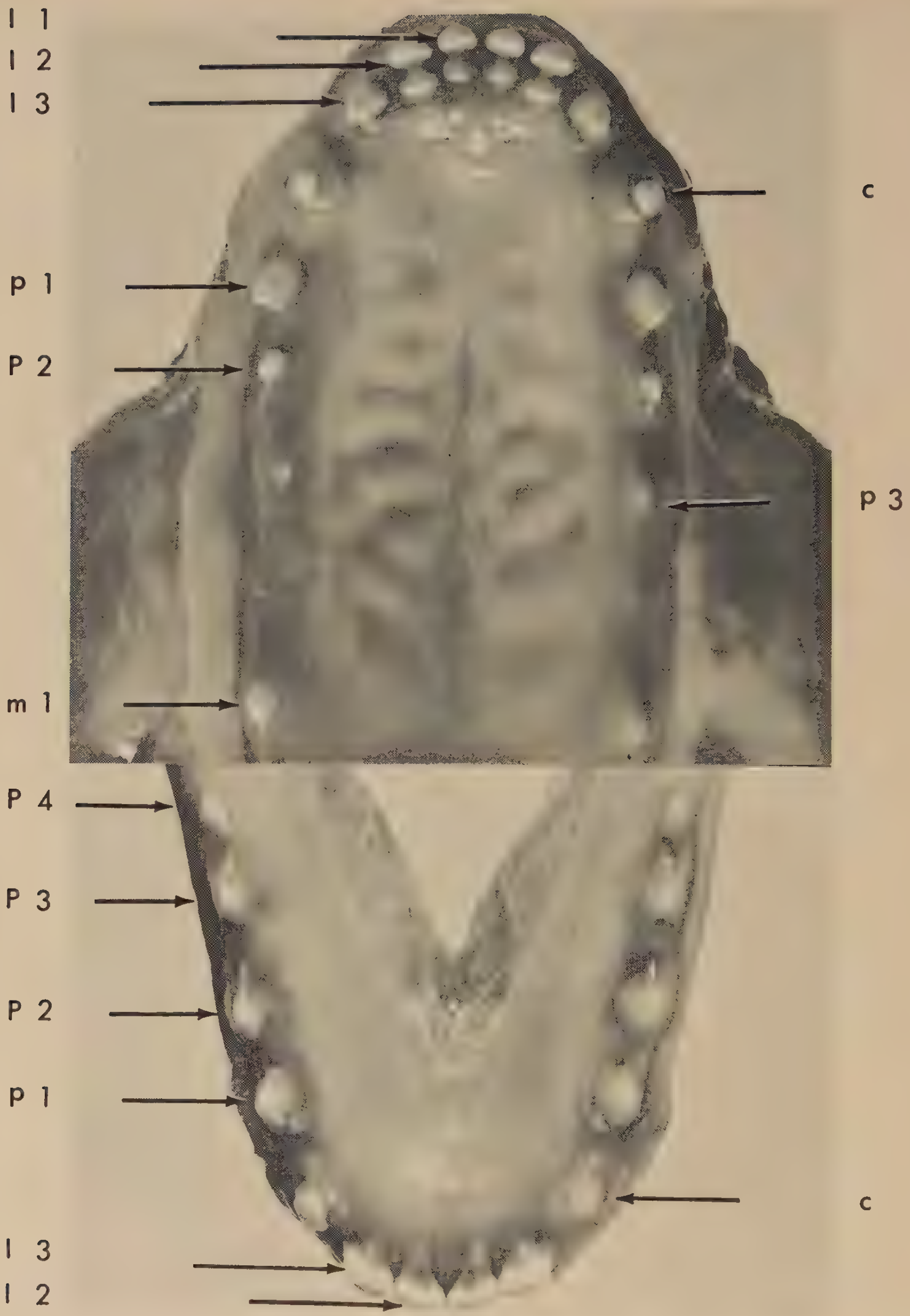
I 1
I 2
I 3
c
p 1
P 2
p 3
m 1
P 4
P 3
P 2
p 1
c
I 3
I 2

PLATE 4.—Deciduous dentition (arrows at right) and permanent dentition (arrows at left) of a full-term fetal male of 4.3 kg., 89 percent MNW. (2078, 2079)

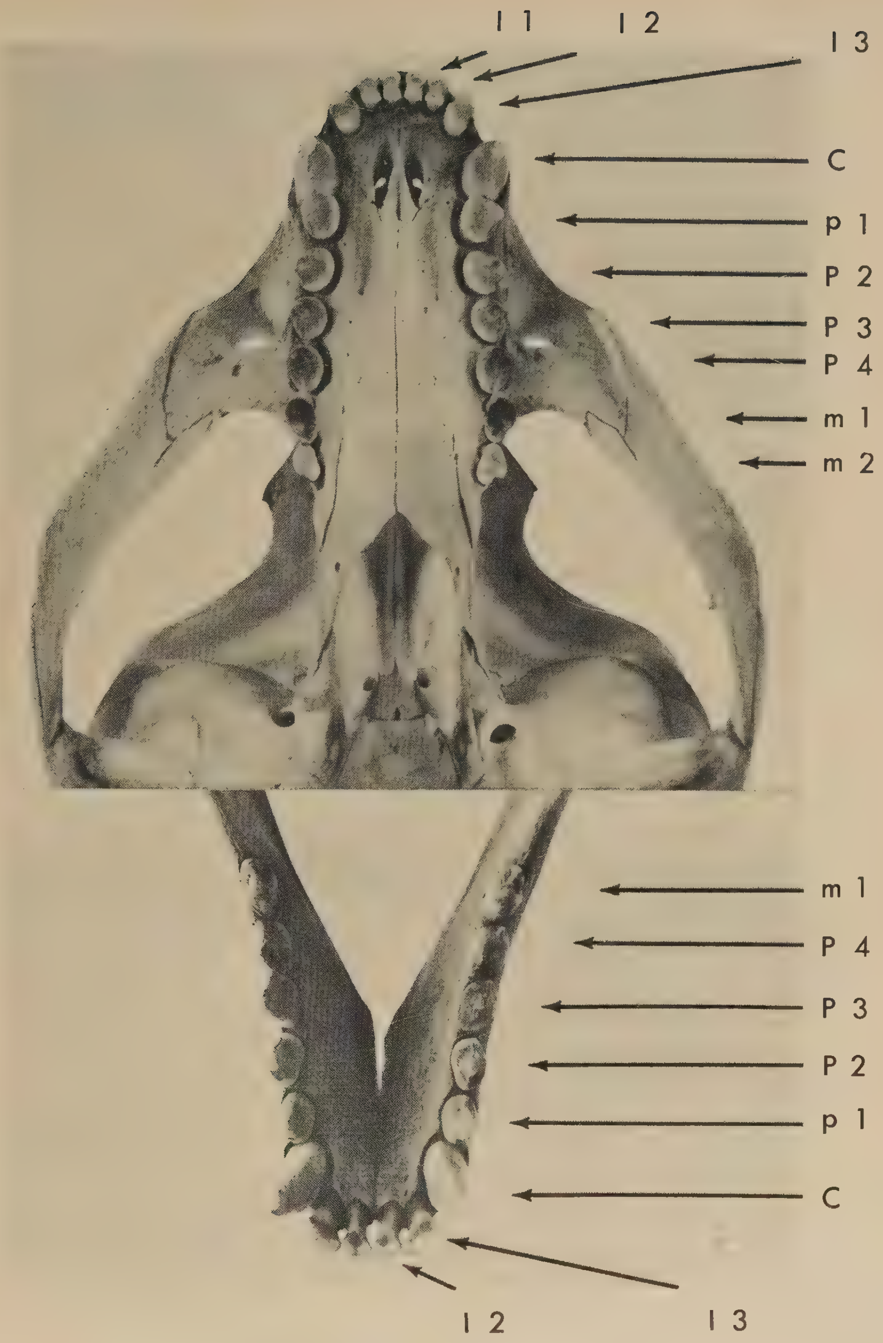
I 1
I 2
I 3
C
p 1
P 2
P 3
P 4
m 1
m 2
m 1
P 4
P 3
P 2
p 1
C
I 2
I 3

Plate 5.—Complete dentition of a female about 7 months old, occlusal aspect. (3041, 4311)

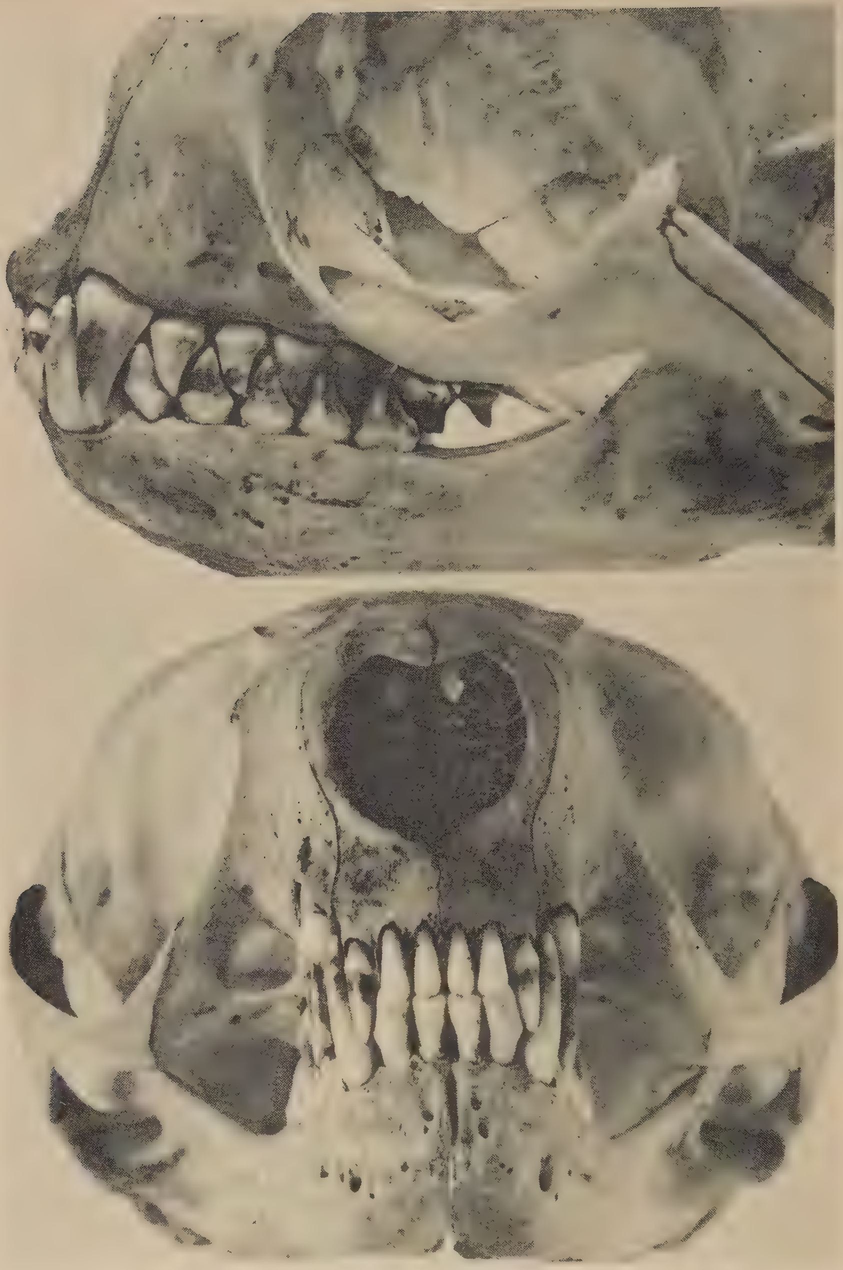

Plate 6.—Complete permanent dentition of a female about 7 months old, lateral and anterior aspects. (Same skull as shown in plate 5.) (4310, 4309)

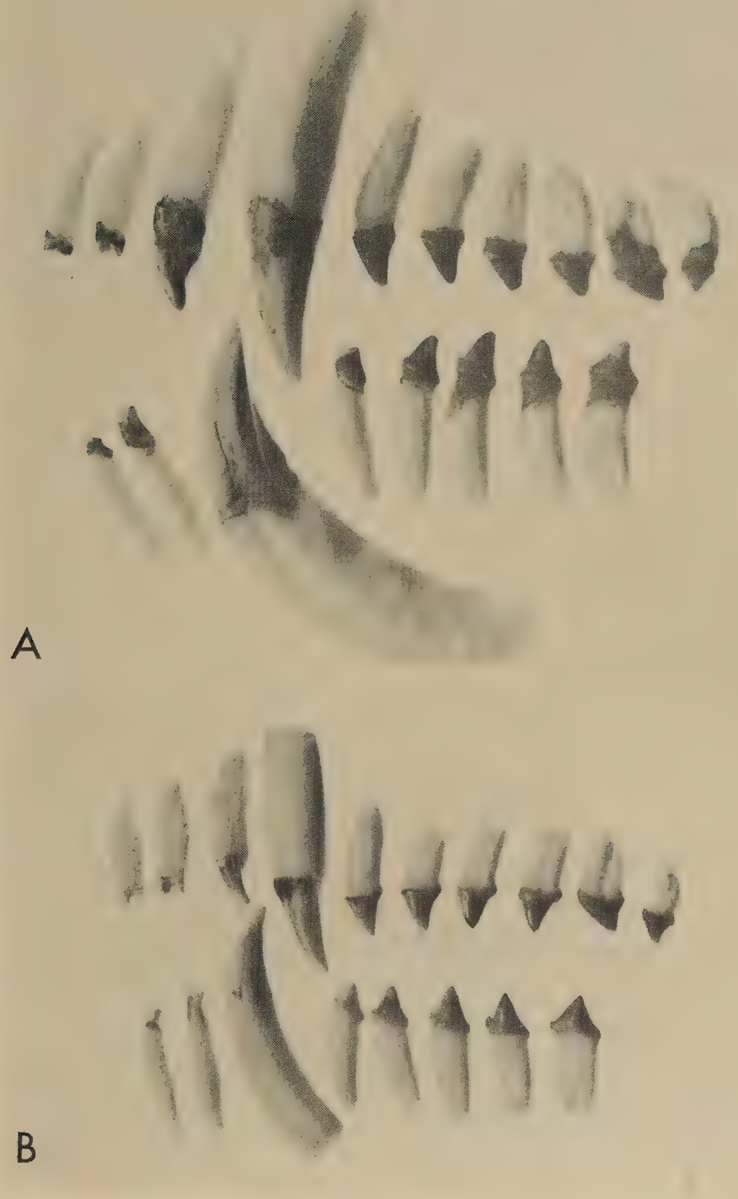

PLATE 7.—Permanent teeth of adults. Left teeth; distal surface of incisors, buccal surface of canines and postcanines; natural size. (A) Male, 10 or 11 years. (B) Female about 6 years. (2430, 2429)

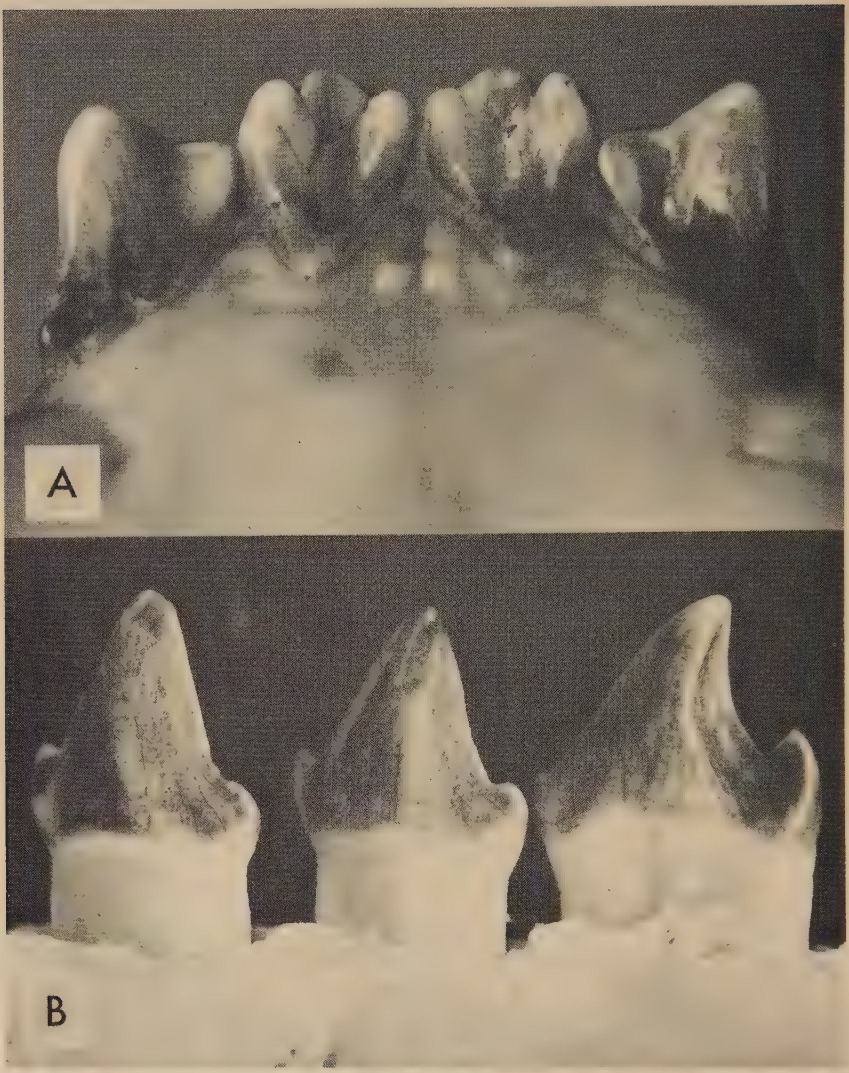

Plate 8.—Shape of cusps of permanent teeth. (A) Lower incisors of 1-month female; lingual surface. (B) Three lower molariform teeth—left P3, P4, and m1—of 7-year female; buccal surface. (4428, 4375)

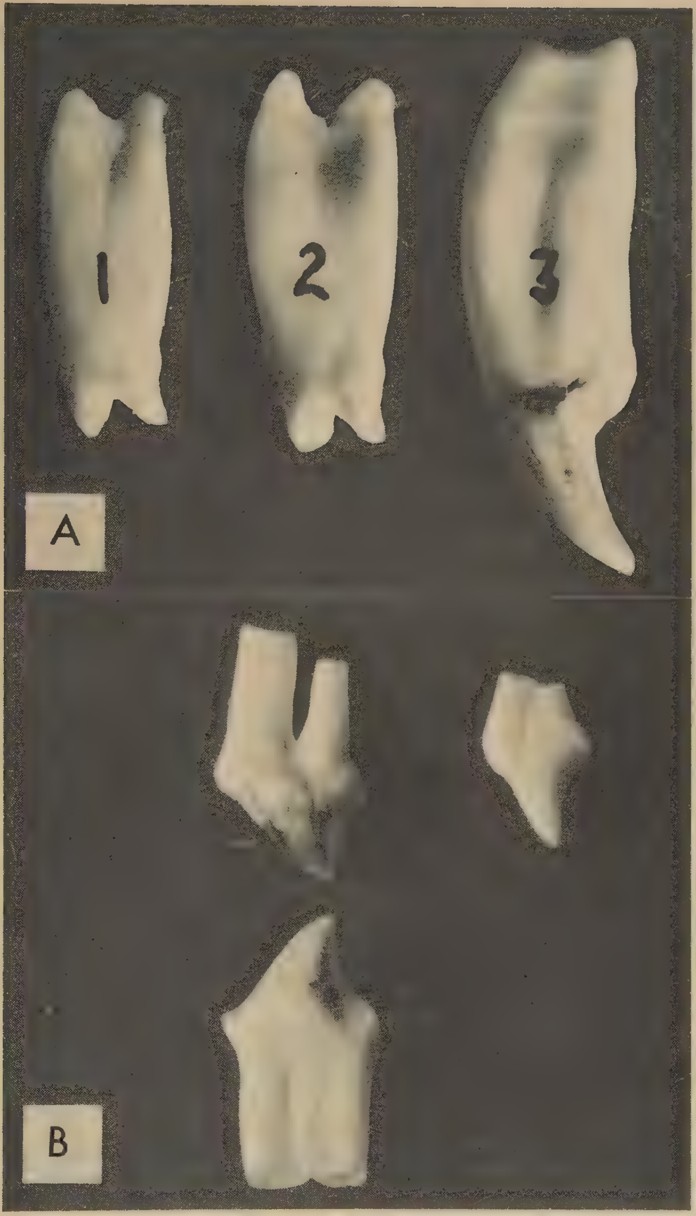

Plate 9.—Shape of roots of permanent teeth. (A) Left upper incisors of 7-year female; distal surface. (B) Roots of left upper m1 and m2, and lower m1, of 3-month female; buccal surface. (4406, 4396)

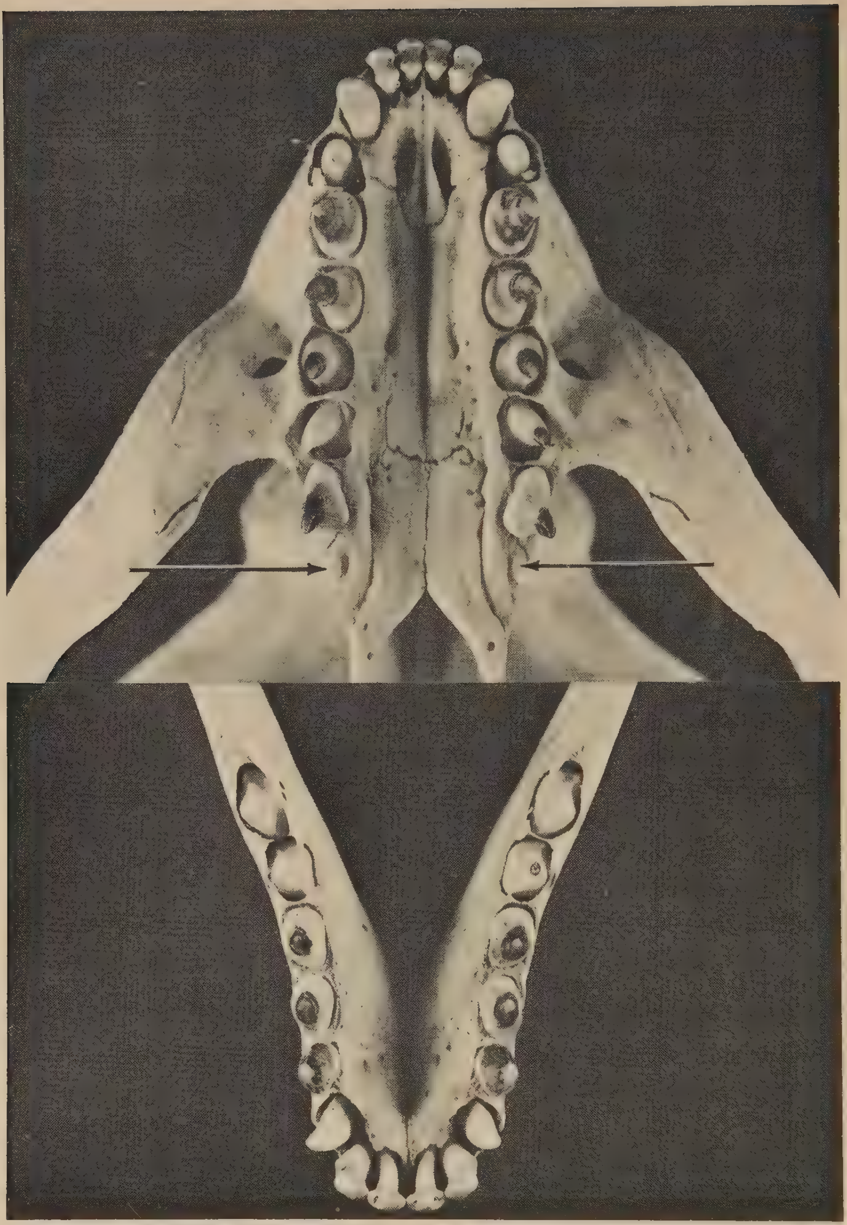

Plate 10.—Permanent dentition, after alveolar eruption, of a female several days old; upper m2 on each side (arrow) has barely erupted; all deciduous teeth have exfoliated. (4339, 4340)

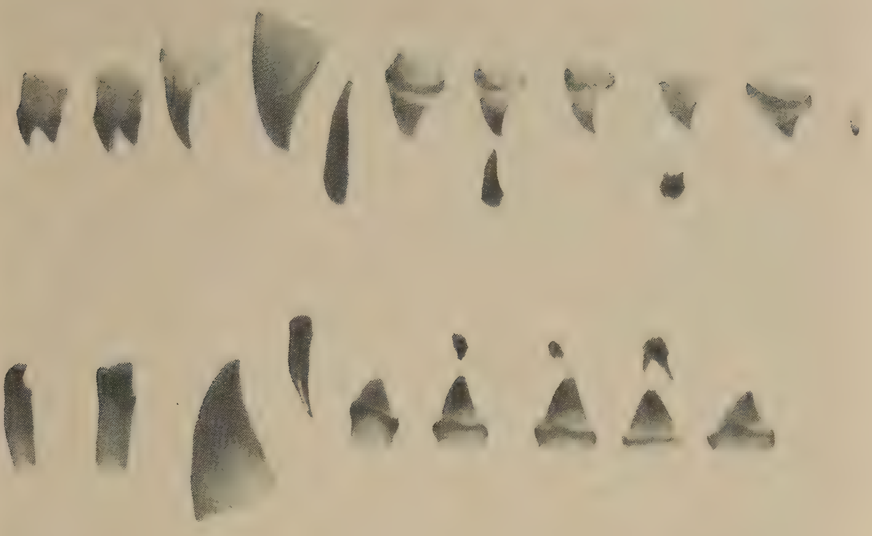

Plate 11.—Permanent teeth and persistent deciduous teeth of a newborn male. Left teeth; distal surface of incisors, buccal surface of canines and postcanines. Seven deciduous teeth persist; upper p3 and all incisors have disappeared. (Lower i3 was present in the right mandible.) (2814A)

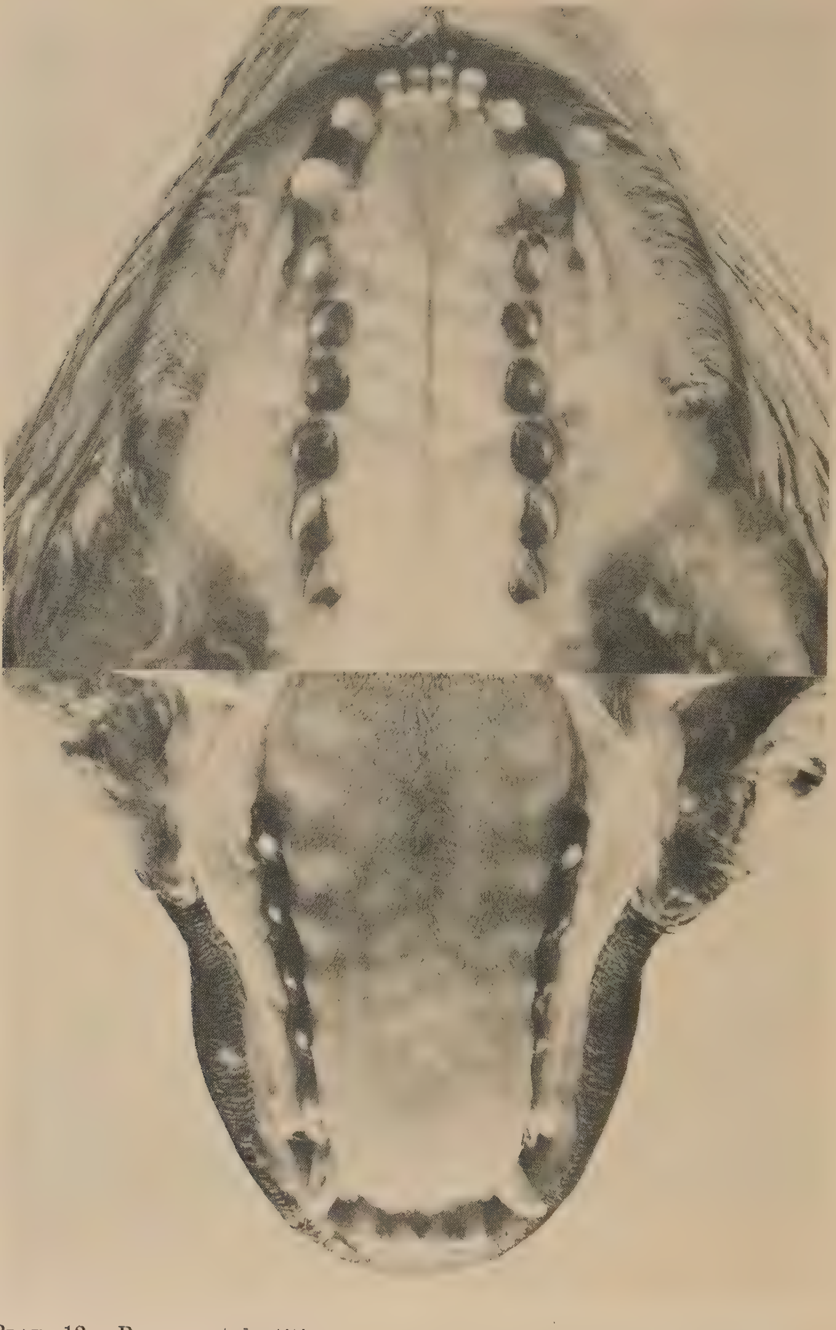

PLATE 12.—Permanent dentition, after gingival eruption, of an 8-month female, March 10, 1960. (4364, 4365)

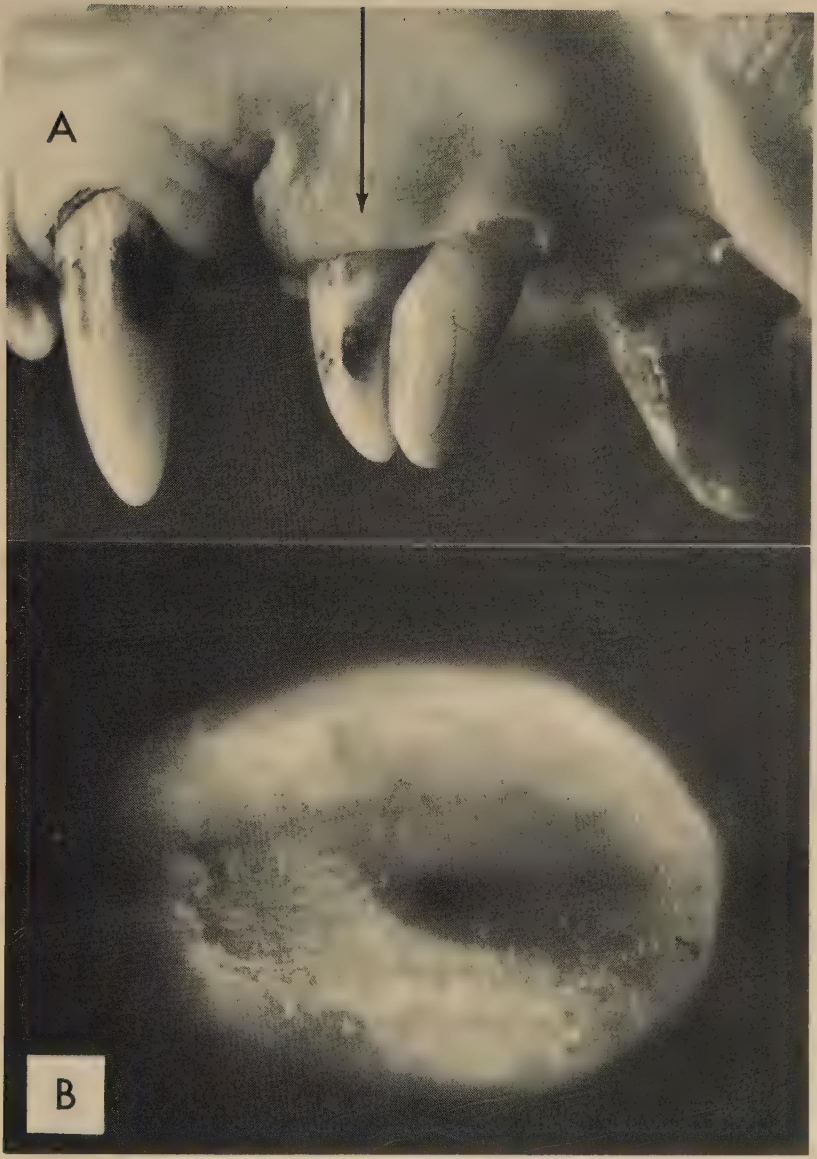

Plate 13.—(A) Upper canines in a mixed dentition stage; arrow indicates left permanent canine erupting along mesiolingual side of deciduous canine, in 1-month female. (B) Closure of root canal in an upper canine of a 12-year female. (4429, 4405)

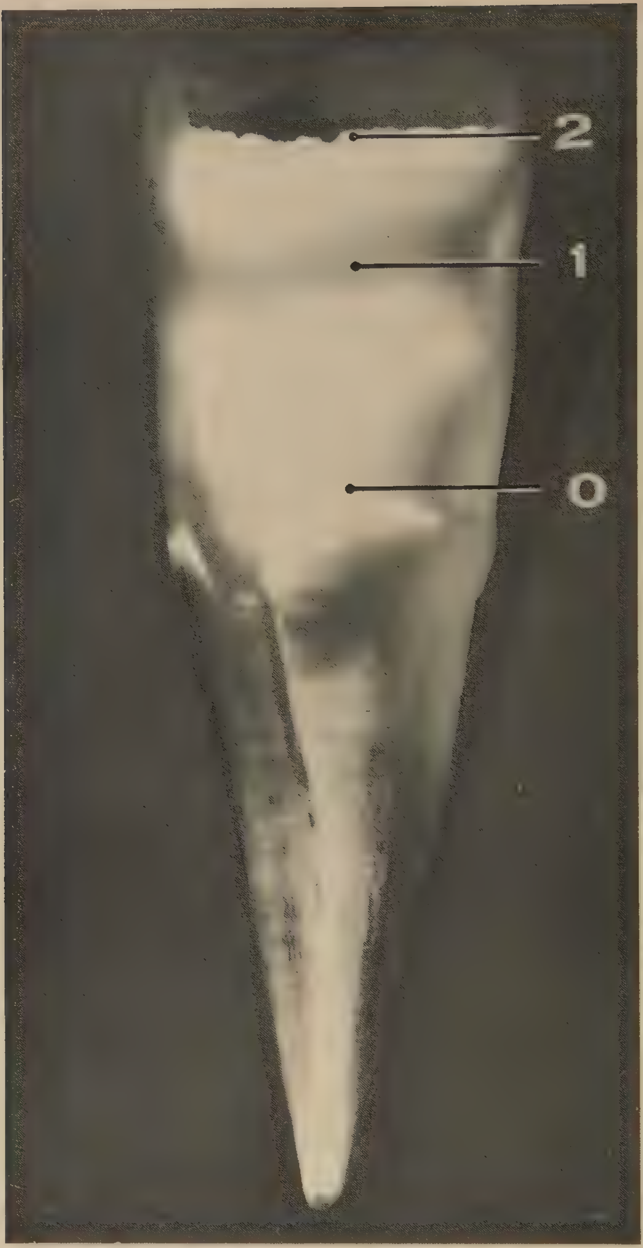

Plate 14.—Annuli on right upper canine of a 2-year male, July 17, 1949; distal surface; ×5. Numbers show approximate position of root base at ages 0 (birth), 1 and 2 years. (2697)

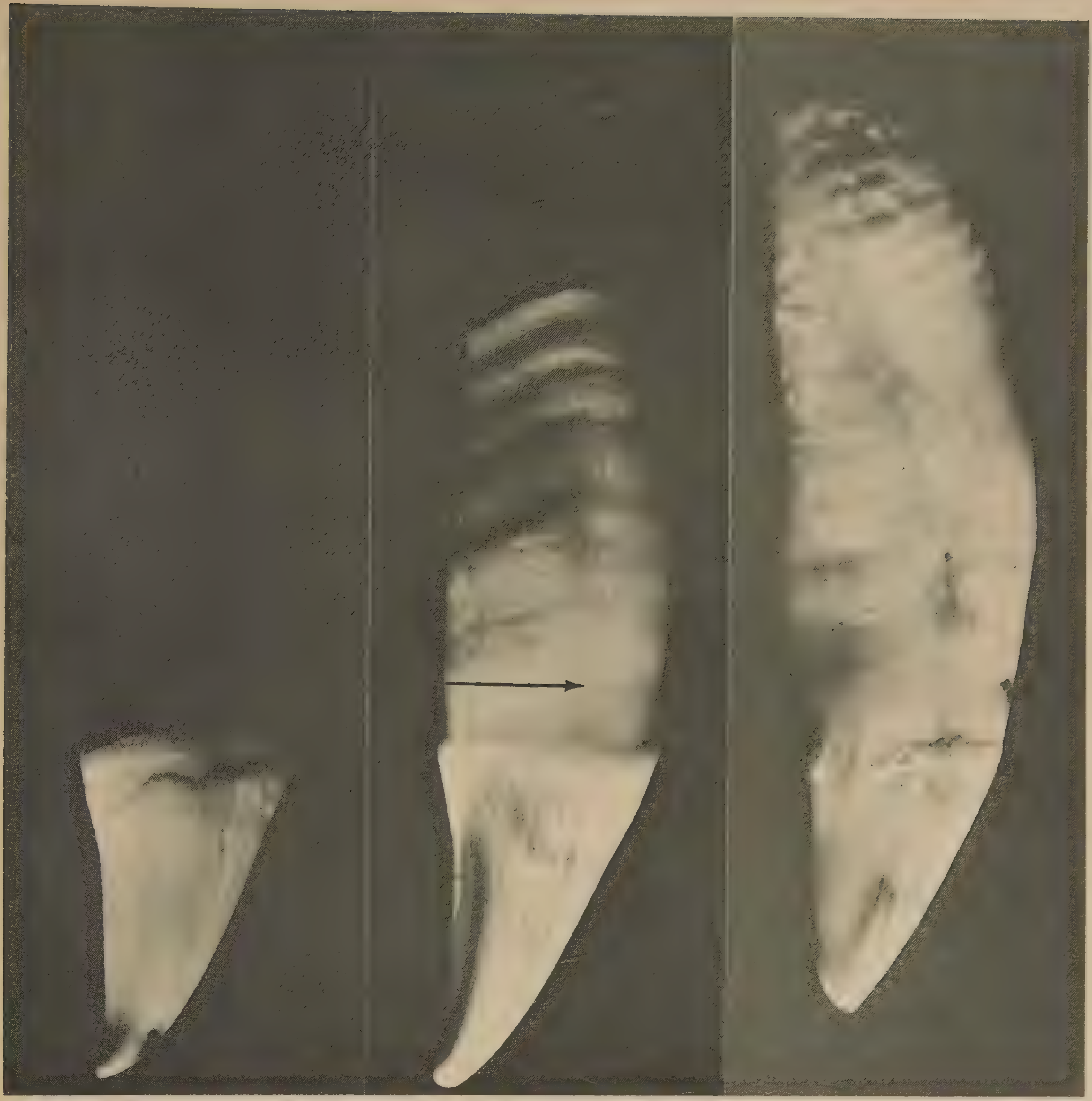

Plate 15.—Annuli on right upper canines of males of three ages; buccal surface. (Left to right) pup several weeks old, killed on 8 August; 6-year-old (tagged), killed on June 17, (arrow points to first-autumn depression); 14-year-old (tagged), killed on July 16. (2701, 2703, 5295)

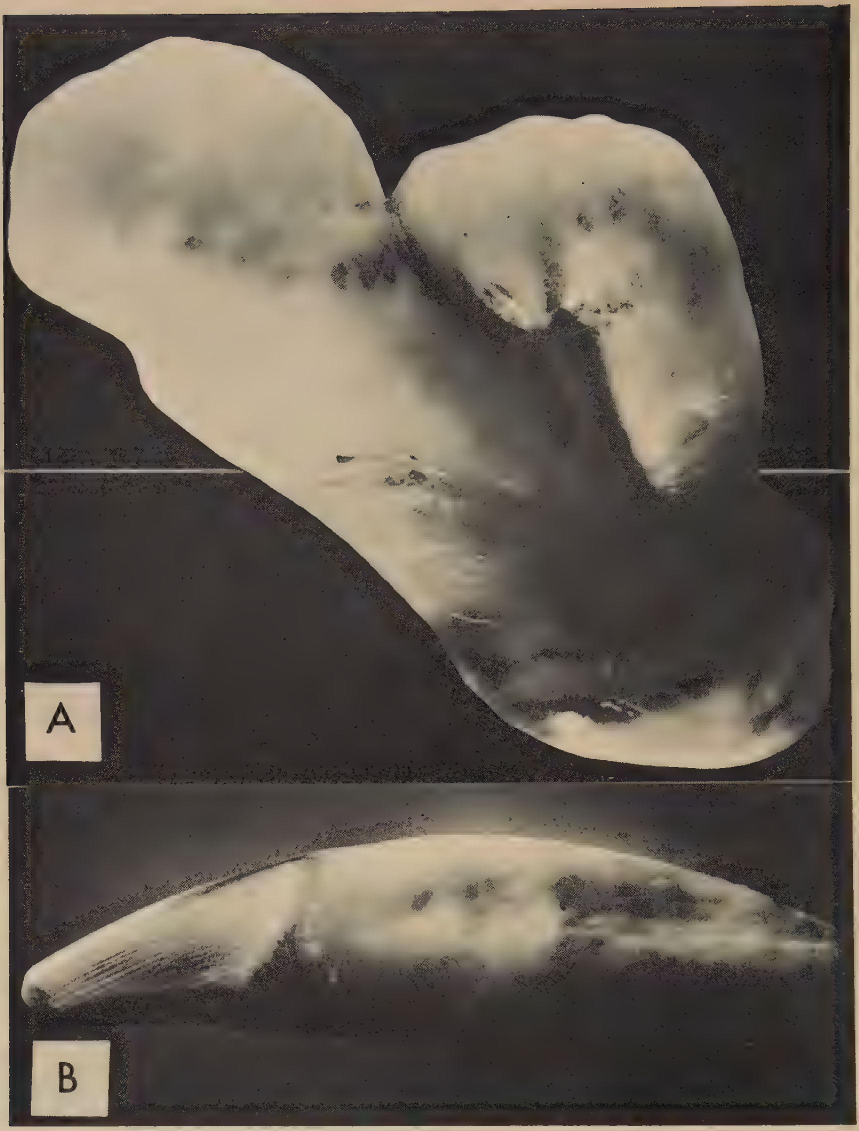

Plate 16.—Cementum on teeth of old adults. (A) Left upper 1st molar of male; buccal surface; white line indicates gum level. (B) Right upper canine of 19-year (tagged) female; lingual surface; crown at left. (4423, 4488)

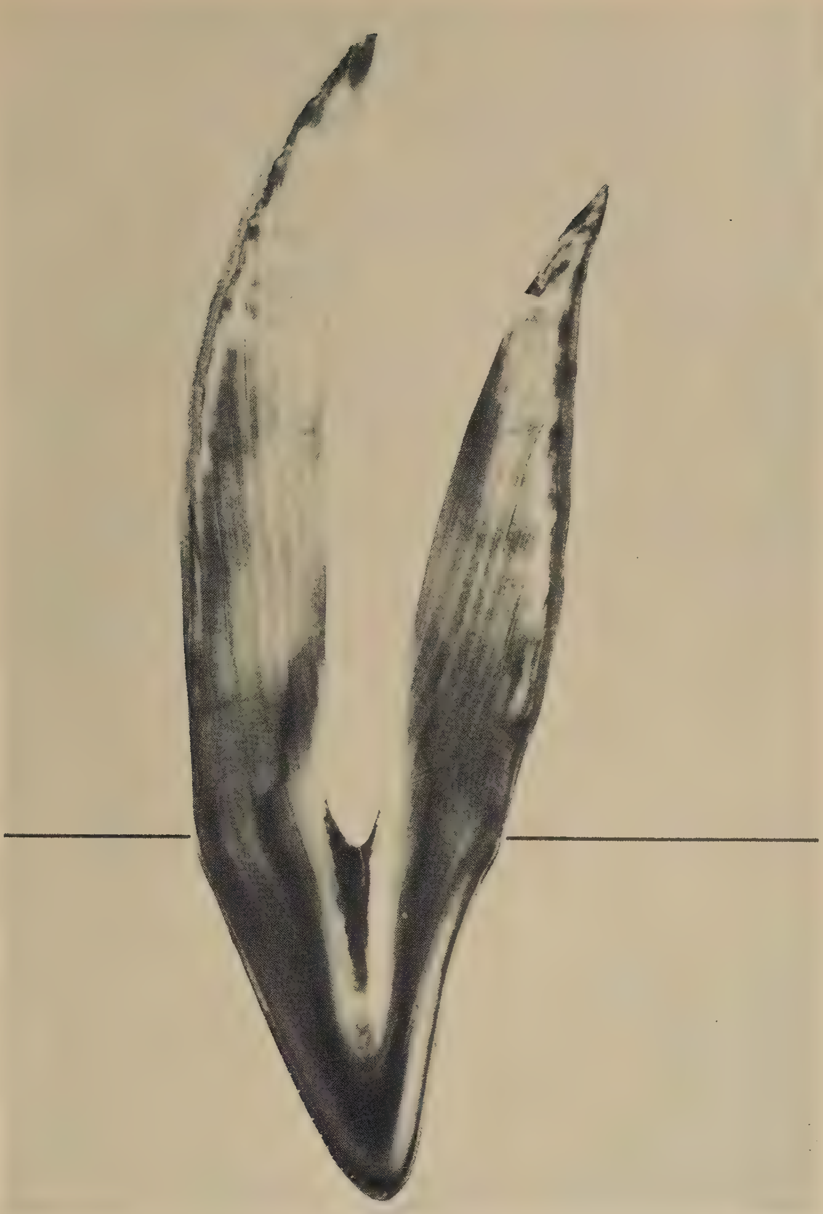

PLATE 17.—Internal structure of right upper canine, showing annuli; median section; 9-year (tagged) male; photographed by UV-excited fluorescence; lingual aspect; line indicates cementoenamel junction. (US 58–737, Mrs. Marion P. Kumpula.)

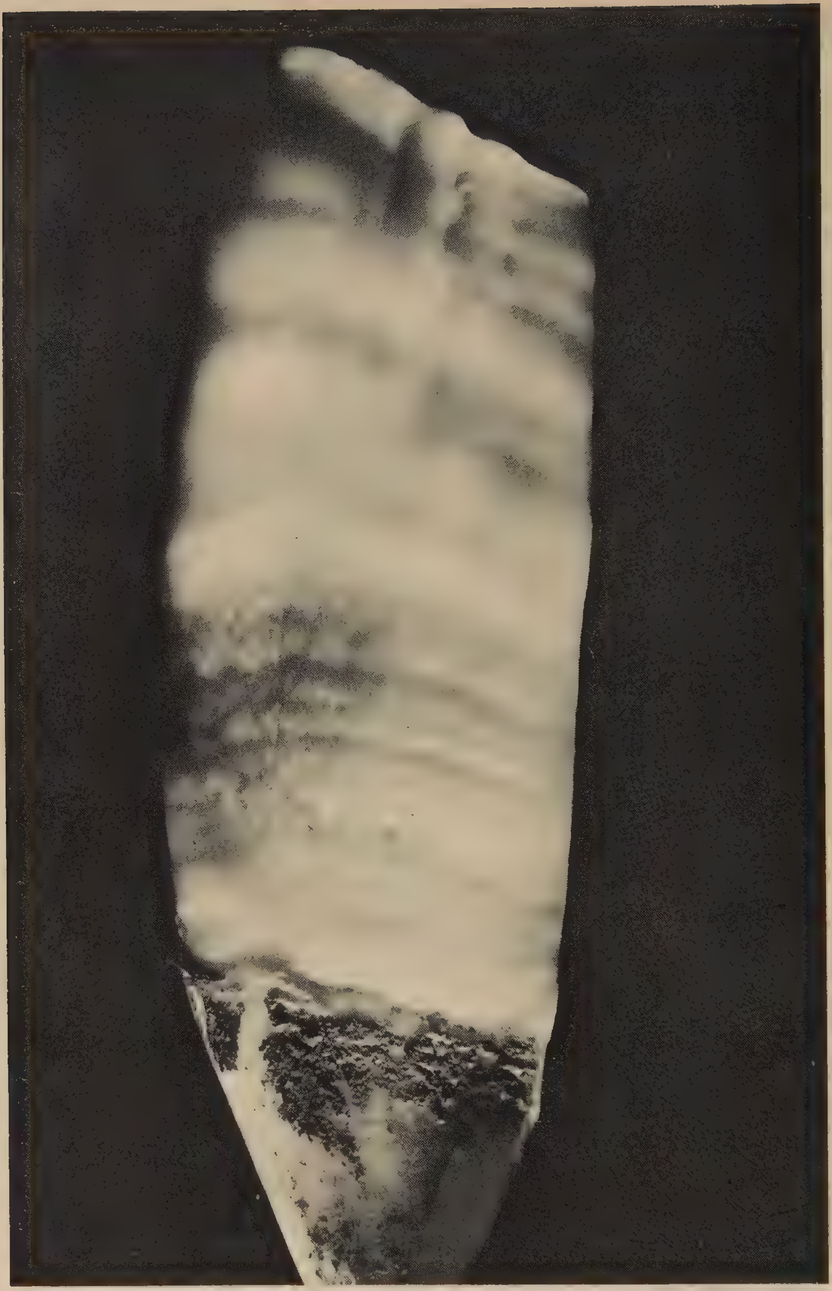

Plate 18.—Annuli on right upper canine of a seal raised in captivity; known age 5-year male; lingual surface. (4487)

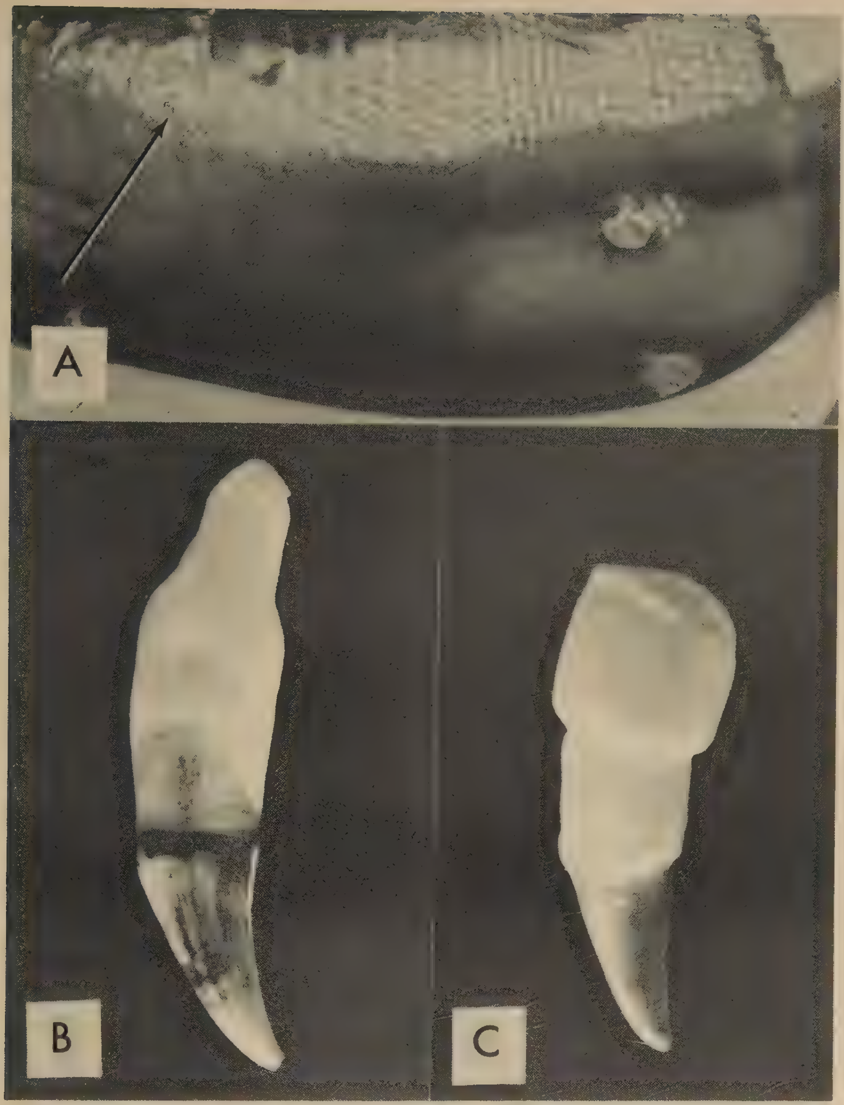

PLATE 19.—Differential growth of the root. (A) Gelatin impression of fine ridges on left lower canine of yearling male; labial surface; cementoenamel junction at arrow; root at right. (B) Left upper canine of female over 10 years old; labial surface. (C) Right upper canine of female, estimated age 4 years; lingual surface. (4409A, 4402, 4403)

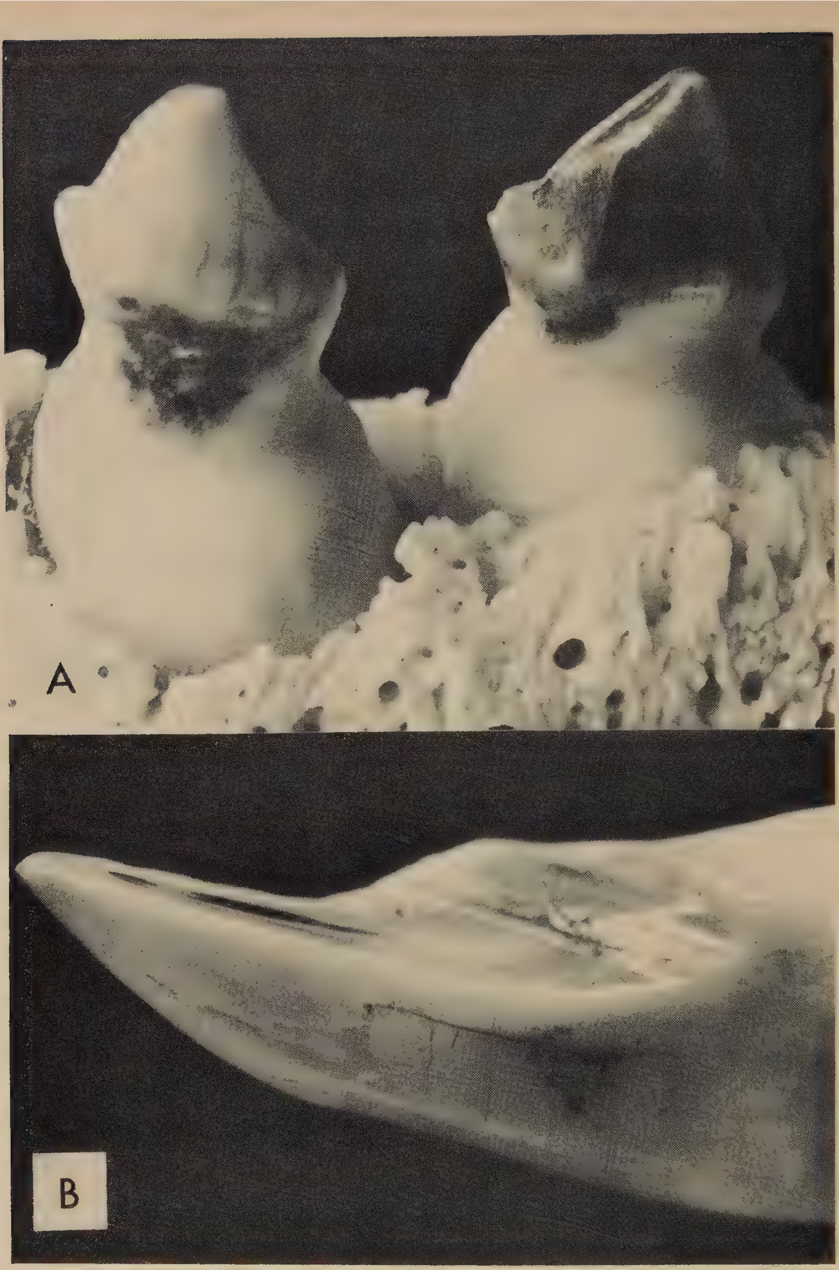

Plate 20.—(A) Appearance in situ of premolars of an 8-year (tagged) male; lower left 1st and 2d; buccal surface. (B) Wear on the crown of the left lower canine of a female over 10 years old; labial surface. (4380, 4404)

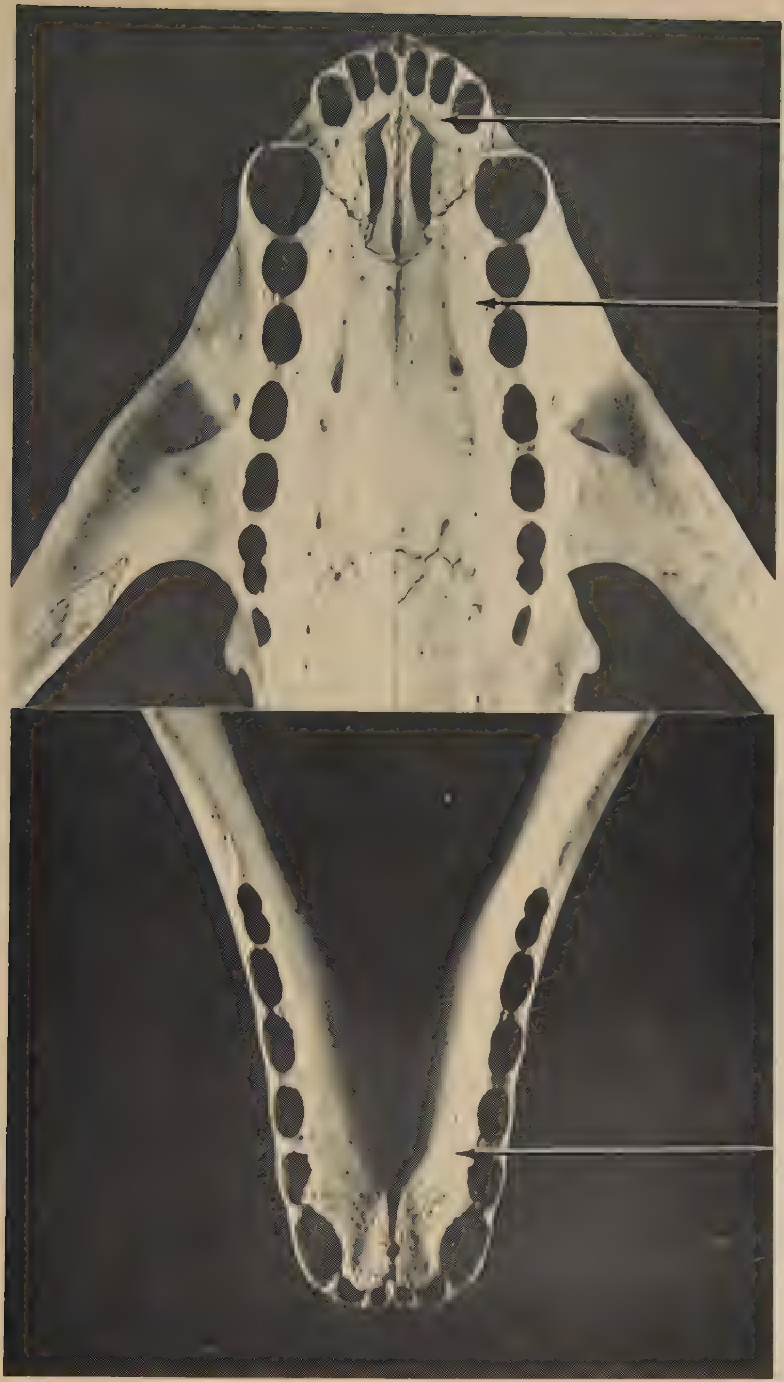

Plate 21.—Jaw bones of a female, estimated age 5 years. Arrows show (top to bottom) premaxilla, maxilla, and mandible. (4410, 4411)

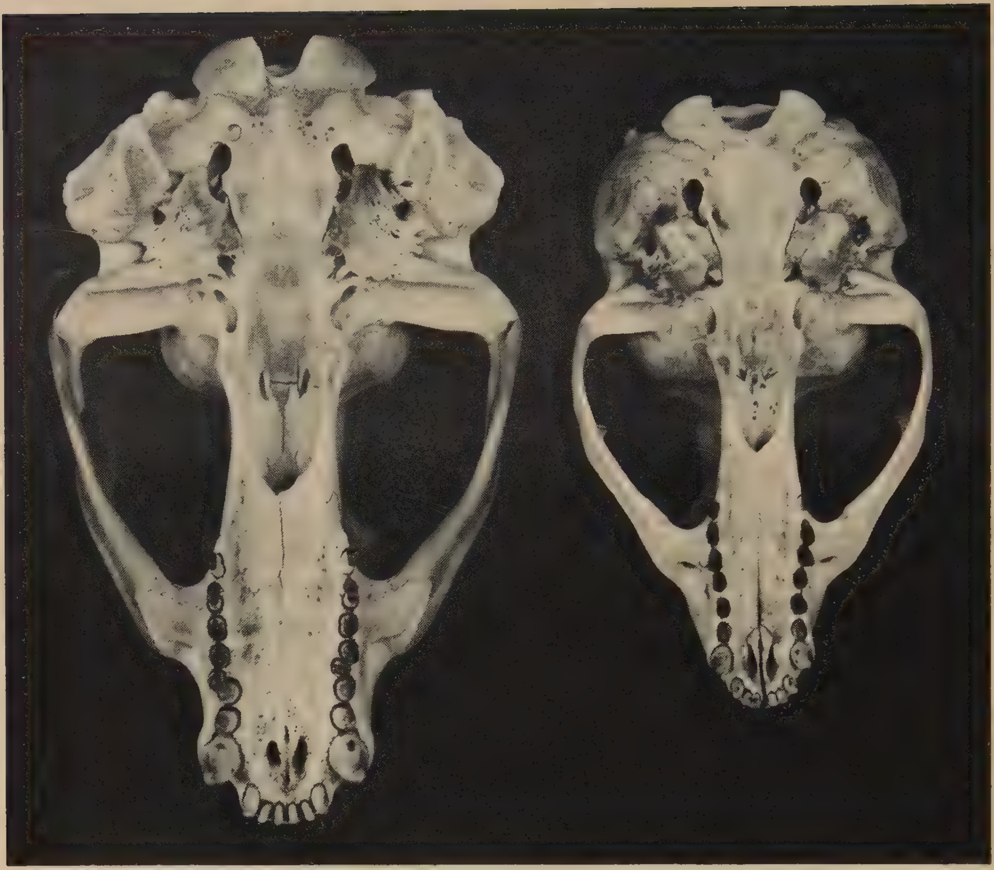

Plate 22.—Skulls of 8-year male and female (both tagged); male (left) condylobasal length 235 mm., female 184 mm. (4494)

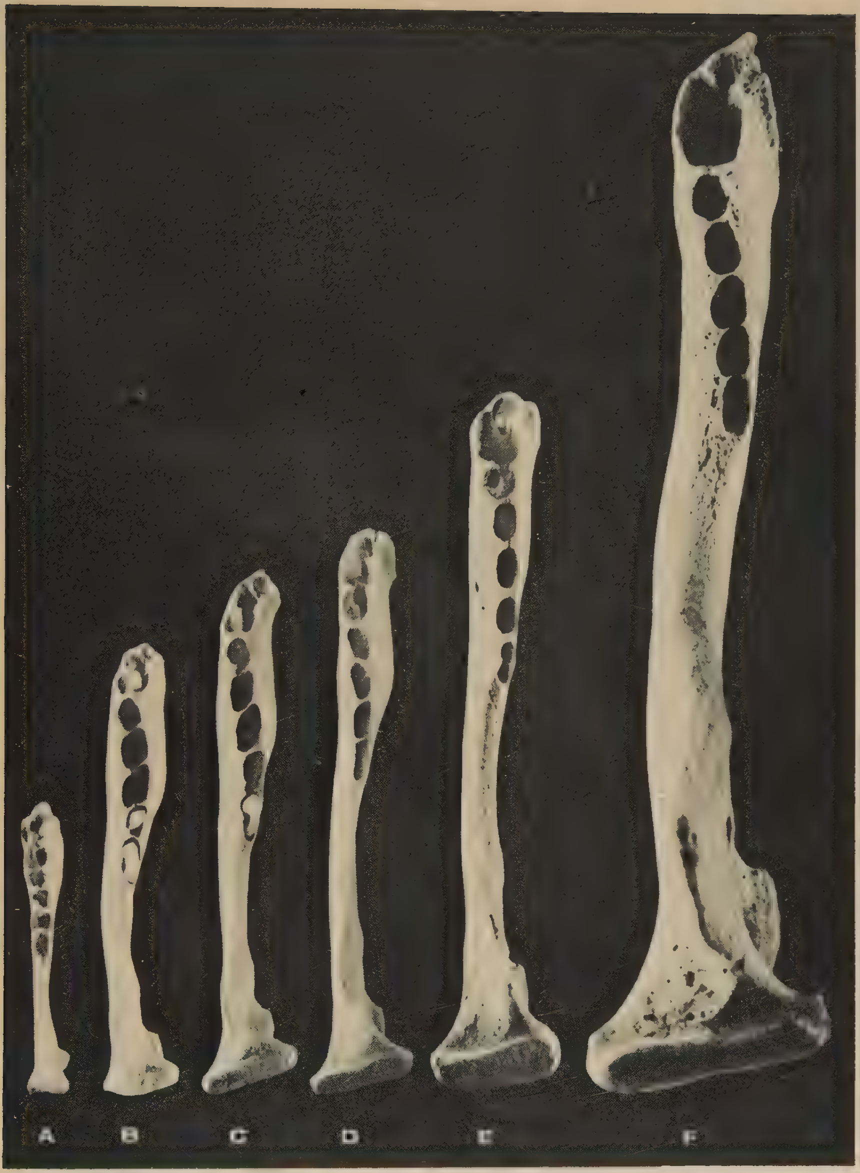

PLATE 23.—Left mandibles of six males, illustrating growth changes with age, natural size. (A) Fetus of 1.36 kg., 25 percent MNW. (B) Fetus of 6.0 kg., 111 percent MNW. (C) Pup 1–2 weeks old. (D) Yearling about 9 months old. (E) Three-year-old (tagged). (F) Old adult. (4426)

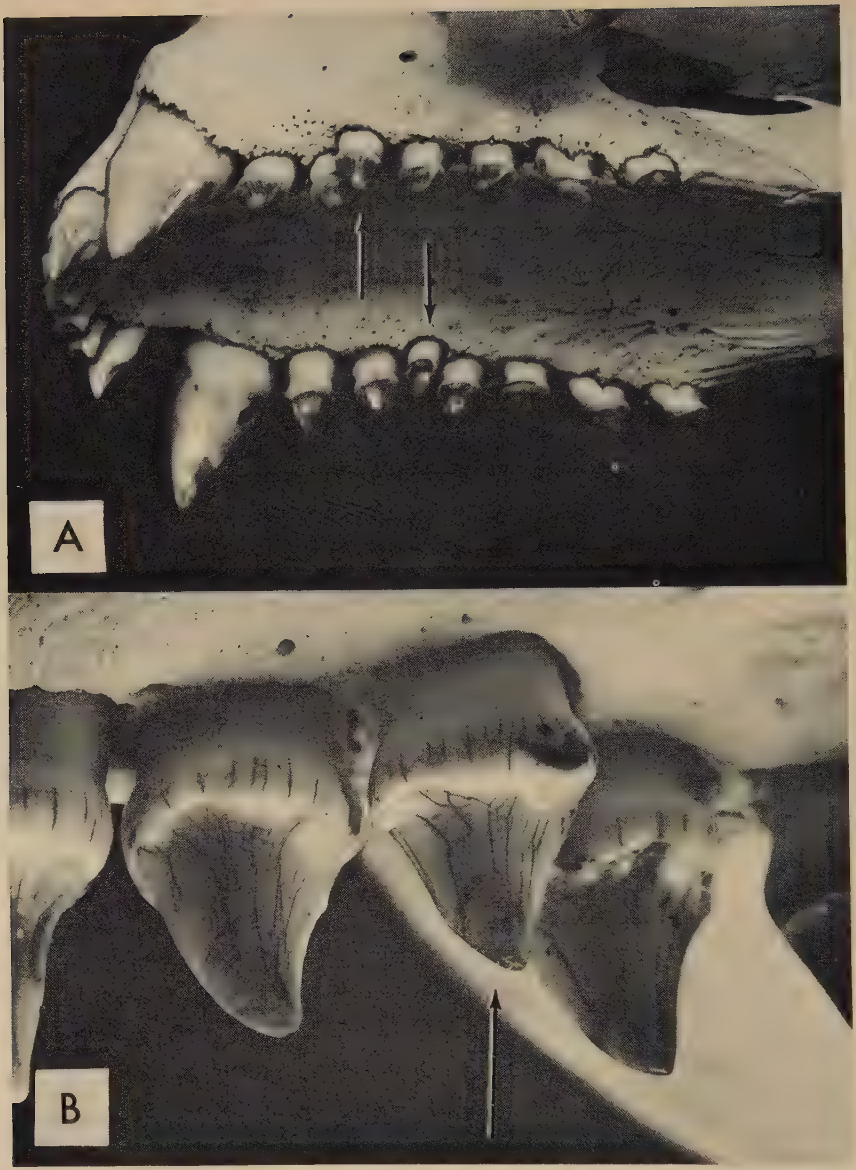

Plate 24.—Extra premolars in two males. (A) Pair between upper P2 and 3 in an 8-year-old (tagged). (B) One of a pair between upper P2 and 3 in a yearling; right jaw; lingual surface. (4374, 4377)

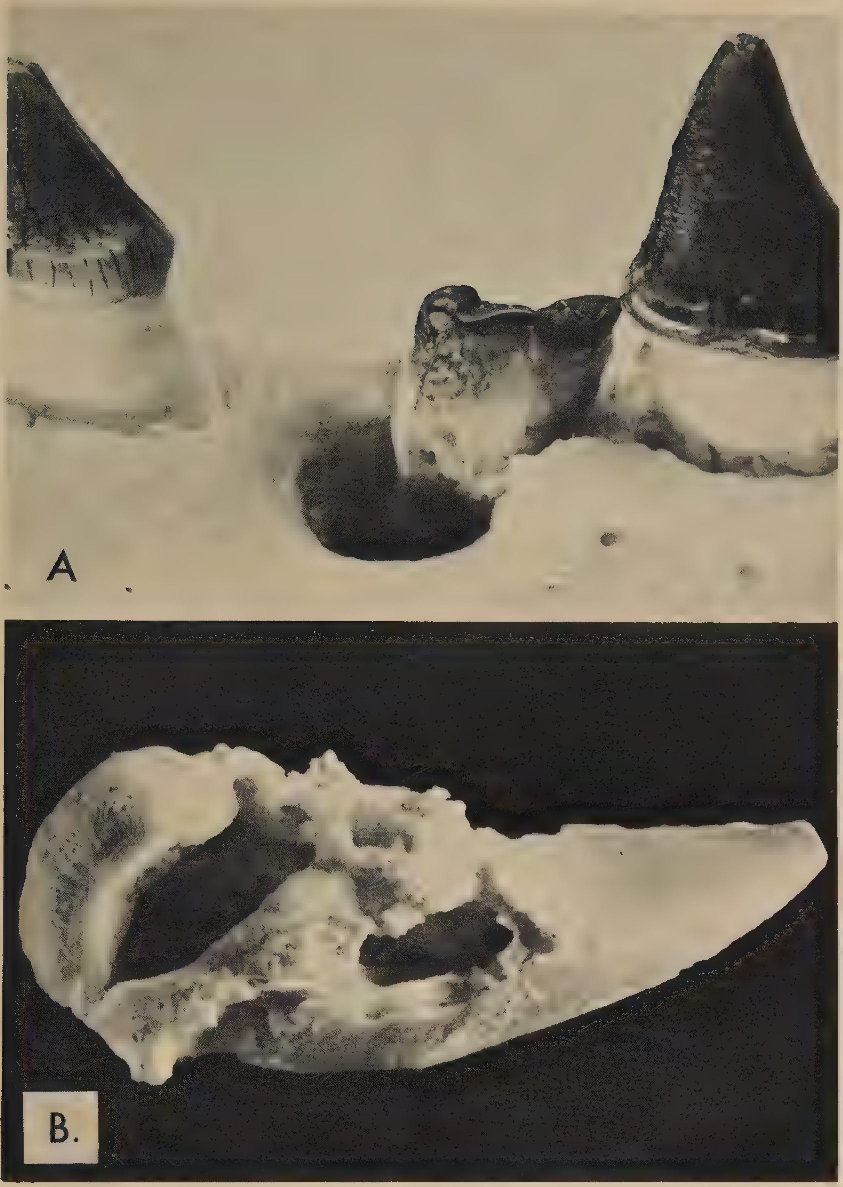

PLATE 25.—Effect of root abscesses on tooth and jaw. (A) Lower right P3 of a 7-year (tagged) female; lingual surface. (B) Upper right canine of a known-age 6-year male raised in captivity; lingual surface. (4378, 4401)

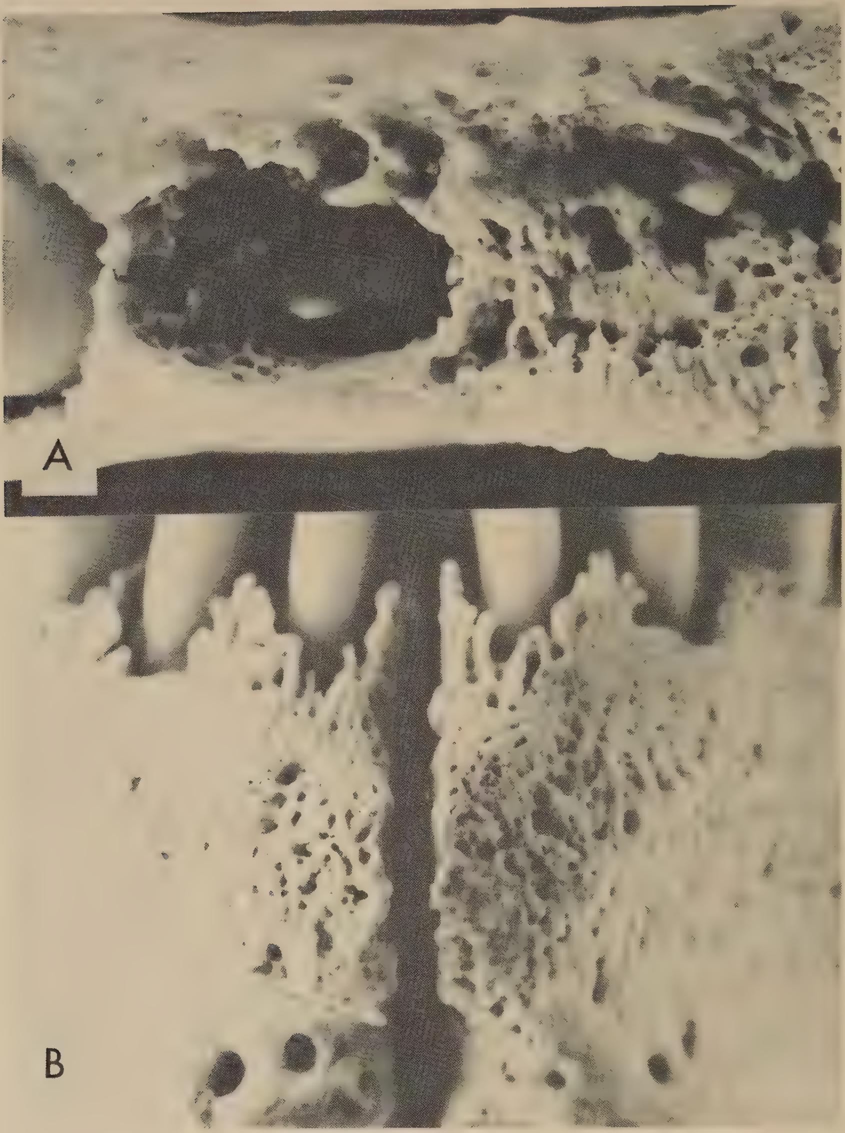

Plate 26.—Spongy bone of the jaw. (A) Left mandible of female over 10 years old; canine at left; all premolars missing; occlusal surface. (B) Mesial end of mandible of 5-year male raised in captivity. (4373, 4376)

A BENTHIC COMMUNITY IN THE SHEEPSCOT RIVER ESTUARY, MAINE [1]

BY ROBERT W. HANKS, *Fishery Biologist*

BUREAU OF COMMERCIAL FISHERIES

ABSTRACT

**The benthos in two selected areas of the Sheepscot
iver estuary, Maine, was surveyed quantitatively
s part of a research program of the Bureau of Com-
iercial Fisheries. A Petersen-type grab obtained 78
ne-tenth square meter samples from the soft mud
ediments. Samples were screened through openings
f 1.5 mm., to separate the macrofauna from micro-
una and sediments.**

The 108 species collected conformed to the description of a *Nephtys incisa-Nucula proxima* community. Fifteen species accounted for 80 percent of the total number of organisms. Variations within the community are described, and some factors that may control size composition in the community are discussed. The Sheepscot infaunal community is compared with the faunal composition of two previously described *Nephtys-Nucula* communities.

In the summer of 1954, Gunnar Thorson of the
Jniversity of Copenhagen invited the Fish and
Vildlife Service to cooperate in quantitative sur-
eys of the level sea bottom [2] fauna. Interest in
ie benthos has increased considerably in recent
ears, and studies of the level-bottom fauna are
ridely established. A benthic survey of the
tlantic coast of the United States and Canada
ould contribute valuable information on coastal
cology, particularly if the survey methods were
omparable with European studies. Knowledge
f benthic populations also contributes to a better
nderstanding of the ecological factors affecting
ommercial species of fish and shellfish. It was
greed to undertake an initial program at the
ureau of Commercial Fisheries Biological Labo-
atory in Boothbay Harbor. The primary objec-
ve was to quantitatively survey the benthic
una in limited areas. Sampling methods were
be established for future shallow-water benthic
udies by the Bureau.

Benthic marine animals are divided into two
cologically different groups described by Petersen
913) and further defined by Thorson (1951, 1956, 1957). The epifauna are those animals living above or on the bottom surface, sometimes attached to rocks, algae, logs, and other solid objects. These organisms are most abundant in the shallow coastal waters, especially in the intertidal zones, and are subject to great variations in environmental conditions. They are usually found in local groups and depend upon the occurrence of suitable substrata for their establishment. The diverse habitat available supports many species within the epifauna. The infauna are those animals that live in the substratum of the gradually sloping (level bottom) portions of the ocean floor. They occupy ". . . more than half the surface of the globe . . ." (Thorson, 1957) and reach their fullest development below the intertidal zone. The infaunal environment is more stable than the epifaunal environment. Characteristically, the

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NOTE.—Approved for publication February 13, 1963.

[1] This paper is based on a thesis submitted to the University of New Hampshire in partial fulfillment of the requirements for the degree of Master of Science.

[2] The "level sea bottom" is the vast uniform area of the continental shelf characterized by a regular slope without abrupt changes in the bottom contour (see Thorson 1957, p. 466).

infauna comprises few genera having an extremely uniform distribution over broad geographical areas, and these animals have become widely used as index organisms in descriptive marine ecology.

The literature relating to benthic fauna has been extensively reviewed by various authors. Jones (1950) has an excellent review of the European literature. Kirsop (1922), Shelford, et al. (1935), and Hartman (1955), among others, have investigated the Pacific fauna. Parker (1956, 1959, 1960) made a detailed series of studies on both the recent and ancient faunal assemblages in the Gulf of Mexico. Atlantic faunistic studies date back to the qualitative surveys of Verrill (1873), followed by those of Kingsley (1901), Sumner, Osborn, and Cole (1913), Cowles (1930), and Allee (1934). Considering that the first truly quantitative benthic survey of any area of the Atlantic coast was not published until 1944 (Lee), advances in recent years are impressive. The New England region is represented in studies by Dexter (1944, 1947), Sanders (1956, 1958, 1960), Wigley (1956), Stickney and Stringer (1957), and Stickney (1959). Sanders' works, together with those of his associates (Wieser, 1960), in Buzzards Bay, Mass., have produced one of the most complete studies on the eastern coast to date. The present paper and that of Stickney (1959) provide a description of the fauna of the Sheepscot River estuary and part of Sheepscot Bay.

PHYSICAL FEATURES OF THE SHEEPSCOT ESTUARY

The Sheepscot River estuary cuts deeply into the Maine coast between Georgetown and Southport Islands (fig. 1). Its mouth, forming Sheepscot Bay, is located at approximately lat. 43°47′ N. and long. 69°42′ W. The lower portion of the estuary extends southward 13.6 miles from the town of Wiscasset to the open sea and varies in width from 2.9 miles to less than 0.1 of a mile. The banks are precipitous in parts of the upper portions of the estuary, and depths of the main river channel vary from about 60 feet at Wiscasset to 166 feet at the mouth. The shores of the lower estuary are exposed bedrock interspersed with mud flats. There are few sandy areas, and the bottom sediments, notably lacking in sand, are composed of a thick, soft, black mud. In places the strong currents have washed away sediments exposing a rocky bottom.

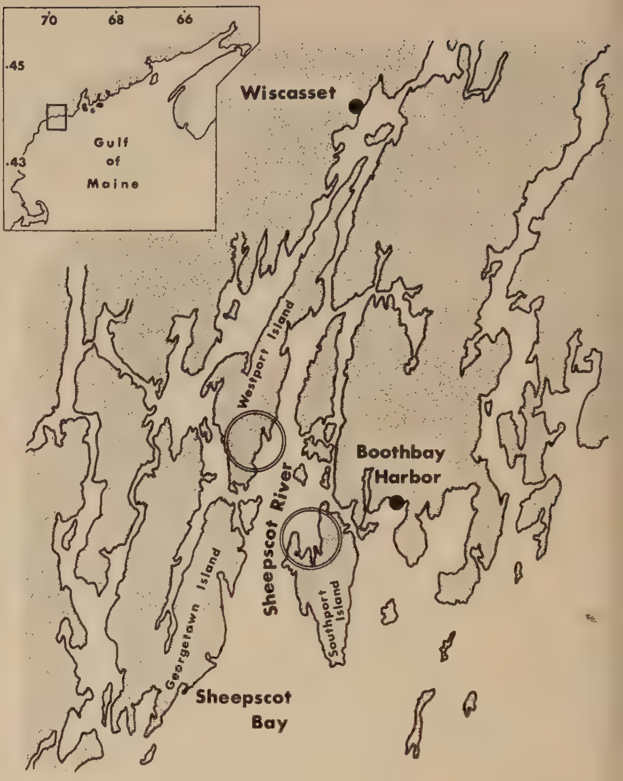
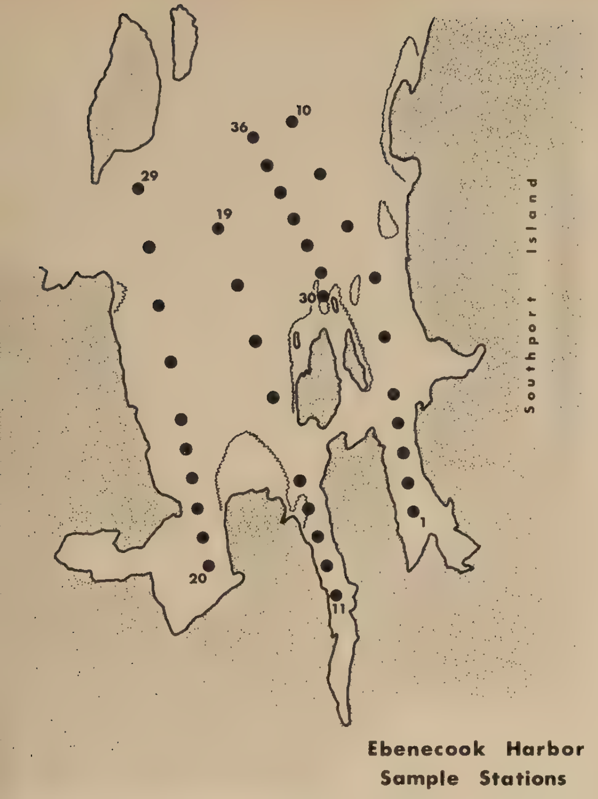


Figure 1.—The Sheepscot River and selected study areas. The upper circle encloses Jewett Cove; the lower circle encloses Ebenecook Harbor. (The small square in the upper left inset is not drawn to scale.)

DESCRIPTION OF EBENECOOK HARBOR

Ebenecook Harbor (fig. 2) is located on the northern end of Southport Island at lat. 43°50′ N. and long. 69°40′ W. There are three parallel coves—Love, Pierce, and Maddock—opening on a narrow, outer channel which forms a convenient northern boundary for the survey area. This channel conducts relatively swift currents into the estuary proper (see fig. 1), and the abrupt channel banks drop to depths of over 100 feet.

Love Cove, easternmost of the three-cove complex, is about 1,050 yards long and 150 yards wide with depths from 4 to 17 feet. Soft mud bottom material is typical with an occasional rocky outcrop. Mud flats cover the head of the cove but most of the shore is exposed bedrock. Pierce Cove is the longest (1,375 yards) of the three coves and has a uniform width of about 100 yards. The shore is rocky with remnants of old, stone wharfs



IGURE 2.—Location of sample stations in Ebenecook Harbor.

two places on the western side. This is a hallow cove, ranging in depth from 3 to 9 feet at ean low water. Past mussel (*Mytilus*) beds are dicated by an accumulation of shells on the soft ottom sediments. Maddock Cove is wider, bout 250 yards, and deeper than the other coves ith similar bottom sediments and shoreline.

The principal source of fresh water comes from ne Sheepscot River, with headwaters located orth of Wiscasset between the Penobscot and ennebec valleys. Near Wiscasset salinities nge from 22 ‰ to 30 ‰ at the surface, while ottom salinities are more constant ranging from) ‰ to 30 ‰. The basis for division of the tuary, upper and lower, and a more detailed escription of the entire area including tidal exhange, salinity and temperature variations, curnts, and biota were discussed by Stickney (1959). ryant (1956) described the river proper. The vo study areas, Ebenecook Harbor and Jewett ove, are representative of the general environental characteristics of the estuary. Salinities ere in the range of bottom salinities cited, and bottom temperatures varied from 10.1° C. to 12.8° C. in Ebenecook Harbor, and from 10.6° C. to 14.7° C. in Jewett Cove.

DESCRIPTION OF JEWETT COVE

Jewett Cove, on the southeastern shore of Westport Island (fig. 3), is about 725 yards from north to south and about 350 yards from east to west. The shoreline in some sections is rocky and drops off sharply into deeper water, while in others it is composed of muddy flats gently sloping into the sea. Midway along the shore there are pilings of a fish weir built out for some distance into the cove. Sampling stations were not located in this area to avoid damage to the weir and possible loss of gear through fouling of lines on the weir stakes. The bottom slopes gradually to depths of 50 feet, beyond which it drops off sharply into the main channel where depths reach 147 feet.

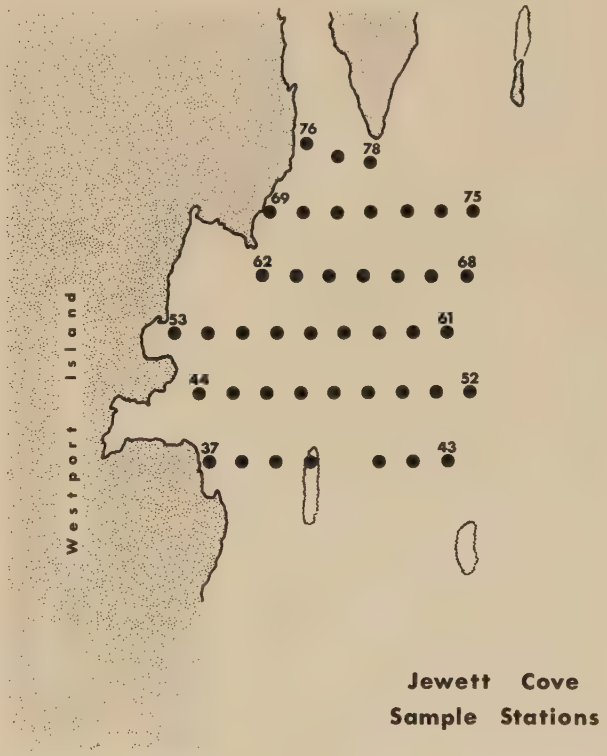


FIGURE 3.—Location of sample stations in Jewett Cove.

APPARATUS AND METHODS

FIELD PROCEDURE

Samples were collected throughout the period of late July to early November in 1955. Both areas were sampled essentially on a grid basis (figs. 2 and 3). Stations were spaced 300 feet apart in shallow water and 600 feet apart in the deeper portions with about 600-foot intervals between adjacent course lines. The stations were located by running the boat on compass courses at a predetermined speed and dropping marker buoys at selected time intervals. Ten different stations were occupied each week with one sample from each of the total 78 stations (table 1). A 28-foot cruiser, with a draft of 3 feet, and a speed of 15 knots, was equipped with winch and pump and used as a sampling platform. The small size was advantageous for shallow-water work, but limited working space and restricted operations to fair weather.

TABLE 1.—*Station data for Ebenecook Harbor and Jewett Cove, Maine, July to November 1955*

Station	Date	Depth, feet	Station	Date	Depth, feet
Ebenecook Harbor:			Jewett Cove—Con.		
1	July 29	3	40	Sept. 15	20
2	do	4	41	do	31
3	do	5	42	do	32
4	do	10	43	do	44
5	do	15	44	Sept. 22	13
6	do	15	45	do	13
7	do	20	46	do	15
8	do	23	47	do	19
9	do	23	48	do	18
10	do	29	49	do	----------
11	Aug. 2	4	50	do	25
12	do	7	51	do	30
13	do	10	52	do	41
14	do	10	53	Sept. 29	14
15	do	9	54	do	14
16	do	15	55	do	15
17	do	22	56	do	16
18	do	24	57	do	20
19	do	26	58	do	21
20	Aug. 8	12	59	do	23
21	do	16	60	Oct. 6	23
22	do	20	61	do	34
23	do	22	62	Oct. 20	20
24	do	27	63	Oct. 6	24
25	Aug. 10	32	64	do	24
26	do	35	65	do	22
27	Aug. 8	35	66	Oct. 20	26
28	do	45	67	do	26
29	Aug. 10	100	68	do	30
30	Aug. 17	14	69	do	20
31	do	23	70	do	26
32	do	27	71	do	25
33	do	27	72	Nov. 8	39
34	do	27	73	do	26
35	do	31	74	do	21
36	do	44	75	do	36
Jewett Cove:			76	do	13
37	Sept. 15	14	77	do	18
38	do	26	78	do	26
39	do	25			

A modified Petersen-type grab (Petersen and Boysen-Jensen, 1911) was used to obtain intact segments of the bottom sediments 0.1 meter square and about 20 cm. in depth (fig. 4). No sample was retained if the dredge was less than two-thirds full. The sample was placed in a screen box (fig. 5), which hung over the side of the vessel, and was washed with water from a pump. The box contained three trays with bottoms of plastic screen; the top screen of 8- by 8-mesh per inch, the next of 14- by 16-mesh, and the bottom tray of 20- by 20-mesh with openings of about 1.5 mm. Organisms were thus separated from sediments by a screen with 1.5 mm. openings; providing an arbitrary division between the macrofauna and microfauna. Each screen retained a portion of the material collected, and this reduced clogging. Clay, silt, and sand were washed through the screens with water, but quantities of broken shell, *Spartina* fragments, gravel, etc., were retained. Organisms collected in the top tray were large enough to remove and classify aboard the boat. The contents of the other two trays were emptied on a collecting board, washed into quart jars, and returned to the laboratory for identification.

Although routine sediment analyses were not made, several random samples were processed through a series of sieves. The finest screen used in this series was 250-mesh per inch (openings of 0.062 mm.). Silt is defined as being composed of particles from 0.05 to 0.002 mm. in diameter (Soil Survey Staff, 1951). Since all of the material in the samples passed through this finer screen, except shell fragments (less than 1 percent), the sediments in the survey areas were considered to be at least 90 percent silt and clay.

Measurements directly related to the sampler, screen size, and sample dimensions are given in the metric system because metric measurements were essential to the experimental design in relating it to other studies.

LABORATORY PROCEDURE

The contents of a quart jar from the field collections were placed in a large, white photographic tray and the organisms picked out by visual inspection. The animals were sorted into five major groups: mollusks, annelids, nemerteans, echinoderms, and miscellaneous. No dead organisms were counted with the single exception of *Volsella modiolus* shells, which were present in large numbers and were uniformily distributed. Epifaunal species were retained for study, but not considered as part of the infaunal association. The organisms were preserved in 10 percent neutralized formalin and later transferred to 70 percent alcohol to prevent deterioration of the calcified parts. Usually no narcotization was used, but when time permitted, or in the case of unusual or rare specimens, particularly polychaetes, coelenterates, and nemerteans, an 8-percent solution of magnesium chloride (isotonic with sea water) was used to relax and extend the animals before fixing. The material gathered each week was stored until the end of the collecting period, when all the organisms from each group were re-examined and identified to species, or to the lowest taxonomic category feasible.

Abundance (number of organisms) has been used as the basis of faunal evaluation for this study. Other factors, such as biomass or dry weight measurements, are recognized as being equally valuable, but were not within the scope of this work. A review of the literature on marine communities will show that the numerical basis of evaluation is not without precedent and one investigator (Sanders, 1960) has supported animal numbers as the most valid measurement.

RESULTS

DISTRIBUTION AND ABUNDANCE

Ebenecook Harbor and Jewett Cove faunas can be considered as one community (table 2) since they differ only in minor aspects. Two species were selected as dominants: the protobranchiate pelecypod *Nucula proxima* Say, the most abundant animal; and the polychaetous annelid *Nephtys incisa* Malmgren, the most uniformly distributed animal. Associated with these dominants are other species that were also evenly distributed in large numbers.

Cumaceans were second in abundance and were

TABLE 2.—*Species in the* Nephtys-Nucula *community found at 10 or more stations in Ebenecook Harbor and Jewett Cove, Maine, and listed in order of abundance*

Rank by number	Species	Number	Number stations	Percent by number	Cumulative percent by number	Percent stations	Average number per square meter	Area [1]	Depth range in survey
									Meters
1	*Nucula proxima*	2,358	59	18.3	18.3	75.6	399.6	E&J	4–30
2	Cumacea sp. (4+species)	1,973	55	15.3	33.6	70.5	358.7	E&J	4–14
3	*Stereobalanus canadensis*	768	34	6.0	39.6	43.6	225.8	E&J	3–31
4	*Thyasira gouldi*	717	46	5.6	45.2	59.0	155.8	E&J	4–31
5	*Phoxocephalus holbolli*	623	39	4.8	50.0	50.0	159.7	E&J	1–9
6	*Volsella modiolus*	573	68	4.4	54.4	87.2	84.2	E&J	1–31
7	*Corophium* sp	557	22	4.3	58.7	28.2	253.1	E, mostly J	0–8
8	*Nucula tenuis*	515	46	4.0	62.7	59.0	111.9	E&J	4–31
9	*Dulichia* sp	407	39	3.2	65.9	50.0	104.3	E&J	5–14
10	*Scoloplos armiger*	402	47	3.1	69.0	60.3	85.5	E&J	4–14
11	*Aricidea* sp	395	43	3.1	72.1	55.1	91.8	E&J	1–14
12	*Nephtys incisa*	332	70	2.6	74.7	89.7	47.4	E&J	1–31
13	*Orchomenella pinquis*	292	28	2.3	79.3	35.9	104.2	E&J	4–14
14	*Ampelisca spinipes*	291	28	2.3	77.0	35.9	103.9	E&J	1–14
15	*Diplocirrus hirsutus*	253	19	2.0	81.3	24.4	133.1	E&J	6–13
16	*Retusa obtusa*	206	48	1.6	82.9	61.5	42.9	E&J	2–31
17	*Sternaspis scutata*	198	31	1.5	84.4	39.7	63.8	E&J	5–31
18	*Hartmania moorei*	155	39	1.2	85.6	50.0	39.7	E&J	5–31
19	*Ampharete acutifrons*	135	42	1.0	86.6	53.8	32.1	E&J	4–31
20	Nemertea sp	134	49	1.0	87.6	62.8	27.3	E&J	----------
21	*Casco bigelowi*	134	16	1.0	88.6	20.5	83.7	E&J	5–8
22	*Nucula delphinodonta*	119	11	.9	89.5	14.1	108.1	E	3–8
23	*Pholoe minuta*	100	40	.8	90.3	51.3	25.0	E&J	4–13
24	*Cingula aculeus*	94	18	.7	91.0	23.1	52.2	E&J	4–14
25	*Crenella decussata*	76	24	.6	91.6	30.8	31.6	E&J	4–31
26	*Lacuna vincta*	75	31	.6	92.2	39.7	24.1	E&J	4–31
27	*Lumbrineris fragilis*	74	40	.6	92.8	51.3	18.5	E&J	4–31
28	*Pherusa plumosa*	66	28	.5	93.3	35.9	23.5	E&J	4–13
29	*Yoldia sapotilla*	66	20	.5	93.8	25.6	33.0	E&J	8–31
30	*Aeginina longicornis*	64	20	.5	94.3	25.6	32.0	E&J	6–14
31	*Ninoe nigripes*	48	27	.4	94.7	34.6	17.7	E&J	4–31
32	*Ammotrypane aulogaster*	34	12	.3	95.0	15.4	28.3	E&J	1–31
33	*Aricidea quadrilobata*	33	14	.3	95.3	17.9	23.5	E&J	1–14
34	*Cerastoderma pinnulatum*	32	17	.2	95.5	21.8	18.8	E&J	3–31
35	*Tellina agilis*	32	19	.2	95.7	24.4	16.8	E&J	1–31
36	*Lora scalaris*	31	20	.2	95.9	25.6	15.5	E&J	4–14
37	*Leptocheirus pinquis*	27	15	.2	96.1	19.2	18.0	J	4–13
38	*Trichobranchus roseus*	27	14	.2	96.3	17.9	19.2	E&J	8–31
39	*Rhodine loveni*	25	16	.2	96.5	20.5	15.6	E&J	4–13
0	*Yoldia limatula*	25	15	.2	96.7	19.2	16.6	E&J	5–10
1	*Nassarius trivittatus*	20	16	.2	96.9	20.5	12.5	E&J	5–31
2	*Phyllodoce groenlandica*	18	12	.1	97.0	15.4	15.0	J	4–13
3	*Terebellides stroemi*	17	14	.1	97.1	17.9	12.1	E&J	5–14
4	*Pitar morrhuana*	16	11	.1	97.2	14.1	14.5	E&J	5–31
5	*Astarte undata*	15	11	.1	97.3	14.1	13.6	E&J	4–31
6	*Priapulus caudatus*	15	11	.1	97.4	14.1	13.6	E&J	6–14
7	*Edotea triloba*	14	11	.1	97.5	14.1	12.7	mostly J	1–13
8	*Sarsiella americana*	11	10	.1	97.6	12.8	11.0	mostly J	1–13
9	Miscellaneous	----------	----------	2.4	100.0	----------	----------	----------	----------

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[1] E=Ebenecook Harbor. J=Jewett Cove.

represented by several species tentatively identified as belonging to the genera *Eudorella* and *Diastylis*. Next in order was the hemichordate *Stereobalanus canadensis*; a selective deposit feeder living in fragile mucus-lined tubes that undoubtedly alter the texture of the sediments considerably. These tubes may also offer habitat for such potentially commensal animals as the amphipod *Corophium* sp. and the polychaete *Hartmania moorei*. *Thyasira gouldii*, a small bivalve, and *Phoxocephalus holbolli*, an amphipod, were fourth and fifth in abundance.

Sixth, in order of abundance, was the bivalve *Volsella modiolus* L. contributing 4.4 percent of all animals and uniformly distributed, occurring at 87.2 percent of the stations. This is a known epifaunal species and cannot be regarded as a member of the Sheepscot infaunal community. The fact that nearly all specimens were dead, zero year class juveniles indicates an adverse habitat for newly metamorphosed individuals of this species.

Nephtys incisa was twelfth in numerical order (2.6 percent) but was found at 89.7 percent of the stations. In this faunal association *Nephtys* is a nonselective deposit feeder burrowing through the upper layers of the sediment, ingesting the substratum from which food materials are obtained. *Nephtys* was selected as a dominant because a *Nephtys-Nucula* community had been described from a similar faunal association (Sanders, 1956) and because *Nephtys* was the most uniformly distributed animal in the Sheepscot survey. The comparatively low abundance may be ascribed to the great numerical fluctuations possible in some benthic communities as indicated by Thorson (1957).

The sampling period, July 29 to November 8, is assumed to have had no effect on the results of the survey, since no drastic environmental changes were observed, nor any important changes in faunal composition: Samples taken later in the year contained the same species typical of earlier samples. Possibly a slight increase in the abundance of some species may have occurred as small juveniles grew large enough to be retained by the screens. However, no change attributable to seasonal factors occurred in the order of species, ranked by abundance, during the survey period.

This, then, is a community of small animals including the bivalves *Nucula* and *Thyasira*, the polychaete *Nephtys*, and the acorn worm *Stereobalanus*. The latter two species provide tubes and tunnels for commensals, such as the scale worm *Hartmania moorei*. Cumaceans and amphipods, particularly *Phoxocephalus*, *Corophium*, and *Dulichia*, are common and may be found as commensals, building tubes, or crawling freely about in the upper layers of bottom material. Most of the organisms are deposit feeders, ingesting the organic materials from the fine ooze layer of the sediments. The numerical abundance of the fauna is concentrated in relatively few species. Fifteen of the 108 species contributed over 80 percent of the total number of organisms. Seven species supplied nearly 60 percent of the animals collected.

This community in the Sheepscot estuary, consisting of approximately 1,500 animals per square meter, is not heavily populated when compared with the 16,000 animals per square meter found by Sanders (1956) in the Long Island Sound community. Possibly the Sheepscot fauna could attain comparable densities. Sanders used a finer screen size (1.0 mm.) for his study which would increase estimates of population density by retaining smaller forms of the dominant species: *Nucula*, *Nephtys*, *Yoldia*, and *Cistenides*.

TABLE 3.—*Occurrence and abundance of selected* species, Ebenecook Harbor and Jewett Cove, Maine, July to November, 1955*

Species	Ebenecook Harbor			Jewett Cove		
	Specimens	Stations	Average number	Specimens	Stations	Average number
	Number	*Number*	*Per m.*^{2}	*Number*	*Number*	*Per m.*^{2}
Nucula proxima	619	19	325.7	1,739	40	434.7
Cumacea sp. (4+species)	828	17	487.0	1,145	38	301.3
Stereobalanus canadensis	158	13	121.5	610	21	290.4
Thyasira gouldi	98	13	75.3	619	33	187.5
Phoxocephalus holbolli	5	4	12.5	618	35	176.5
Volsella modiolus	129	27	47.7	444	41	108.2
Corophium sp	3	1	30.0	554	21	263.8
Nucula tenuis	73	11	66.3	442	35	126.1
Dulichia sp	188	12	156.6	219	27	81.1
Scoloplos armiger	173	17	101.7	229	30	76.3
Aricidea sp	272	19	143.1	123	24	51.2
Nephtys incisa	132	32	41.2	200	38	52.6
Orchomenella pinquis	4	4	10.0	288	24	120.0
Ampelisca spinipes	252	14	180.0	39	14	27.9
Diplocirrus hirsutus	4	4	10.0	249	15	166.0
Retusa obtusa	98	18	54.4	108	30	36.0
Sternaspis scutata	55	10	55.0	143	21	68.0
Hartmania moorei	48	13	36.9	107	26	41.1
Ampharete acutifrons	21	11	19.0	114	31	36.7
Nemertea sp	28	16	17.5	106	33	32.1
Casco bigelowi	3	2	15.0	131	14	93.5
Nucula delphinodonta	119	11	108.1	--------	--------	--------
Pholoe minuta	18	10	18.0	82	30	27.3
Cingula aculeus	10	3	33.3	84	15	56.0
Crenella decussata	6	3	20.0	70	21	33.3

*First 25 from table 1.

COMMUNITY VARIATION

Although the two small areas studied produced nearly identical fauna, certain species were not found in both areas, and there were marked differences in occurrence and abundance (table 3). Greater average numbers of animals per sample were obtained in Jewett Cove than in Ebenecook Harbor (223.8 vs. 105.6) and more species per sample (24.9 vs. 14.8) were taken. The faunistic differences that exist between the two areas were found in fringe species that are incidental to the community (table 4). For example, 16 species were obtained in Jewett Cove that were not found in Ebenecook Harbor and Ebenecook Harbor provided 19 species not found in the other area. In Ebenecook Harbor, 15 of the 19 species were annelids, 2 species were mollusks, and 2 species were intertidal (epifaunal) gastropods. Only nine of the species in Jewett Cove were annelids, five were mollusks, and two were arthropods. Most of these animals were found in such small numbers that they appear to contribute little to community structure, but some species from each area were important to the bottom fauna. They were *Nucula delphinodonta* in Ebenecook Harbor and a three-species complex of the genus *Corophium* in Jewett Cove. *Corophium* was particularly important in the total abundance providing .3 percent of all fauna (table 2). Although *N. delphinodonta* contributed only about 1 percent to the combined fauna, the concentrated occurrence must be important in the bottom associations of the deeper regions of Ebenecook Harbor, possibly in competition with *Nucula proxima.*

TABLE 4.—*Species not found in both Ebenecook Harbor and Jewett Cove, Maine, July to November, 1955*

Ebenecook Harbor		Jewett Cove	
Species	Number	Species	Number
Annelida:		Annelida:	
Polycirrus medusa	2	*Eunoe nodosa*	7
Polycirrus eximus	5	*Goniada maculata*	1
Praxillura ornata	3	*Flabelligera affinis*	2
Heteromastus filiformis	3	*Scalibregma inflatum*	4
Capitella capitata	3	*Maldane sarsi*	13
Eteone longa	1	*Praxillella praetermissa*	6
Phyllodoce mucosa	1	*Phyllodoce groenlandica*	18
Nereis virens	12	*Euchone rubrocincta*	1
Nereis caudata	1	*Nereis pelagica*	1
Aricidea sp. 1	3	----------	----------
Paraonis gracilis	2	----------	----------
Polydora sp.	1	----------	----------
Streblospio benedicti	57	----------	----------
Nephtys caeca	9	----------	----------
Prionospio malmgreni	1	----------	----------
Mollusca:		Mollusca:	
Nucula delphinodonta	119	*Clinocardium ciliata*	4
Yoldia myalis	2	*Mytilus edulis*	2
Littorina littorea	3	*Lyonsia arenosa*	1
Littorina saxatilis	5	*Lyonsia hyalina*	1
----------	----------	*Cylichna alba*	8
		Arthropoda:	
----------	----------	*Leptocheirus pinquis*	27
----------	----------	*Anonyx lilljeborgii*	6

The faunal differences may be ascribed to physical and environmental conditions. Both Ebenecook Harbor and Jewett Cove were sampled essentially on the same grid plan. Ebenecook Harbor enclosed an area of 8,139 square meters, from which 36 one-tenth square meter samples were obtained, and Jewett Cove contained an area of 7,113 square meters, from which 42 one-tenth square meter samples were taken. Ebenecook Harbor is a more sheltered environment away from the main currents of the Sheepscot River and depends primarily on tidal exchange for circulation. Distinct environmental differences may be observed among the three coves in Ebenecook Harbor, probably as a result of their isolation from each other. Studies on the annual fluctuations in green crab, *Carcinus maenas*, populations have shown that winter mortalities—attributable to climatic factors—may be confined to one cove, but not necessarily the same cove, in successive years (W. R. Welch, oral communication). Jewett Cove, however, is hardly more than an indentation in the western bank of the Sheepscot River. The currents washing over the bottom are more pronounced than those in Ebenecook Harbor, water mass exchange may be more rapid, and probably more food material is available. These factors may also present an opportunity for a greater number of planktonic larvae to be brought into the area, and possibly provide for a more homogeneous distribution of the established animals. Differences in bottom slope, steeper in Jewett Cove and tending to compress the horizontal range of species with narrow depth requirements, may also be an important agent controlling faunal distribution.

DISCUSSION

Size composition

Apparently large animals are at a disadvantage in this community of small organisms and cannot establish themselves in this habitat. The marked small size of almost all animals in the *Nephtys-Nucula* community merits discussion, particularly with regard to some factors favoring small animals in this situation.

The possibility exists that the sampling equipment may not capture large animals either because the animals live beyond the depth of sediment to which the grab can dig, or because the animals are too widely scattered. Neither of these appear to be valid objections, since the equipment has obtained larger animals from other local communities in soft sediments and other types of samplers have been used on the *Nephtys-Nucula* community without obtaining significant numbers of large animals (Sanders, 1956, 1960; Stickney and Stringer, 1957).

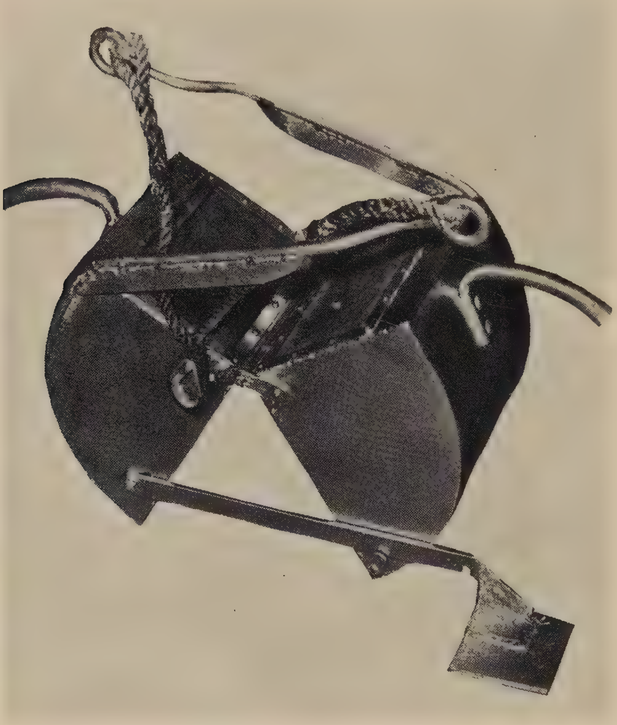

FIGURE 4.—Petersen-type dredge similar in construction to the grab used in this survey.

If the apparent size composition is not influenced by limitations of sampling then other selective factors must be operative. Juveniles of potentially large animals are occasionally taken in the sampler (for example, *Pitar morrhuana* at 11 stations), but these animals rarely reach mature size in this community. The advantage gained by superior numbers alone may be favorable to small animals in the competition for habitat and the ability to mature rapidly can be very advantageous in colonization. High natality, rapid growth, and early maturity enables the species within a population to fill the ecological niche rapidly tending to exclude species with the slow growth and late maturity characteristic of many large animals. If predation should become a dominant factor in controlling community size-composition, slow growth and late maturity expose prey to longer periods of predation and fewer individuals will reach adulthood. Recruitment of large animal species in the *Nephtys-Nucula* community tends to be at long intervals from sources outside the occupied area while recruitment is intensive and at shorter intervals from the endemic, smaller species.

Sediments conducive to the establishment of a population of small infaunal animals are probably not favorable to large organisms from the outset. Soil particle size may be an important selective factor in determining the size range of organisms in the community. The physical and chemical modifications (fecal deposition, tube construction, particle selection, etc.) of such sediments by a community of small animals would be expected to make the environment less attractive the longer the community successfully maintained itself.

Other environmental and ecological factors may regulate size composition within any animal community, and further research on this subject is needed.

Geographical distribution

The *Nephtys-Nucula* community was first described by Sanders (1956) from the benthos in Long Island Sound. Originally termed the *Nephtys incisa-Yoldia limatula* community, *Nucula* being rejected as a dominant because of small size, the name has been revised in recent papers on the basis of further study and now stands as *Nephtys incisa-Nucula proxima*. Sanders (1958, 1960) has also found the *Nephtys-Nucula* community in the soft mud bottoms of Buzzards Bay, Mass. He pointed out in these papers that although *Nephtys incisa* has often been classified as a carnivore, it is a nonselective deposit feeder in this association. This is particularly important if the animal is used to typify the community since predators are not considered to be stable members of an infaunal association (Thorson, 1957).

Stickney and Stringer (1957) have reported a faunal association from the soft mud bottoms of Greenwich Bay, R.I., which appears somewhat transitional between Sanders' *Ampelisca* community and the *Nephtys-Nucula* community. The *Ampelisca* community does exist in a large part of

Table 5.—*Comparison of four* "Nephtys-Nucula" *communities*

Rank	Sheepscot River	Buzzards Bay [1]	Long Island Sound [2]	Greenwich Bay [3]
1	*Nucula proxima*	*Nucula proxima*	*Nephtys incisa*	*Ampelisca spinipes.*
2	Cumacea sp	*Nephtys incisa*	*Nucula proxima*	*Corophium cylindricum.*
3	*Stereobalanus canadensis*	*Ninoe nigripes*	*Yoldia limatula*	*Podarke obscura.*
4	*Thyasira gouldi*	*Cylichna orzya*	*Cistenides gouldi*	*Tharyx acutus.*
5	*Phoxocephalus holbolli*	*Callocardia* [=*Pitar*] *morrhuana*		*Tornatina canaliculata.*
6	*Volsella modiolus*	*Hutchinsoniella macracantha*		*Spiochaetopterus oculatus.*
7	*Corophium* sp	*Lumbrinereis tenuis*		*Macoma tenta.*
8	*Nucula tenuis*	*Turbonilla* sp		*Nucula proxima.*
9	*Dulichia* sp	*Spio filicornis*		*Pitar morrhuana.*
10	*Scoloplos armiger*	*Retusa caniculata*		
11	*Aricidea* sp	*Dorvillea caeca*		
12	*Nephtys incisa*	*Tharyx* sp		
Sediment	Very high percent silt-clay	Very high percent silt-clay	Greater sand content than other surveys.	Highly modified by Ampelisca tubes.
Equipment	Petersen-type Grab	Foster Anchor Dredge (modified).	Foster Anchor Dredge (modified).	Hayworth clamshell.
Sample size	0.1 m.² x 10 cm. deep	7.6 cm. deep—calculated surface area from volume.	7.6 cm. deep—calculated surface area from volume.	0.5 m.² x 30 cm. deep.
Finest screen	1.5-mm. openings	0.2-mm. openings	1.0-mm. openings	2.0-mm. openings—subsample only (0.5 m.² x 8.0 cm.) remainder through 12-mm. openings.

[1] From Sanders (1960). [2] From Sanders (1956). [3] From Stickney and Stringer (1957).

Greenwich Bay, but there is a strong indication from sedimentary and faunal evidence, that at least a section of the center part of the Bay could support the *Nephtys-Nucula* community.

The *Nephtys-Nucula* community has been recorded therefore from three locations on the Atlantic coast: Long Island Sound, Buzzards Bay, and Sheepscot Bay, with the possibility of a fourth in Rhode Island. These communities are compared in table 5. Characteristically, they are composed of small deposit-feeding species which live in the top few centimeters of the bottom sediments where a supply of organic food materials provides nutritional support for relatively large numbers of short-lived, but early maturing animals. The community appears to be endemic to the northern coasts of the United States in relatively protected bodies of water and is confined to the soft mud bottoms which have a high silt-clay sediment composition. The animals which it comprises are generally boreal. Species composition of minor community organisms will vary depending on the geographical location of the population.

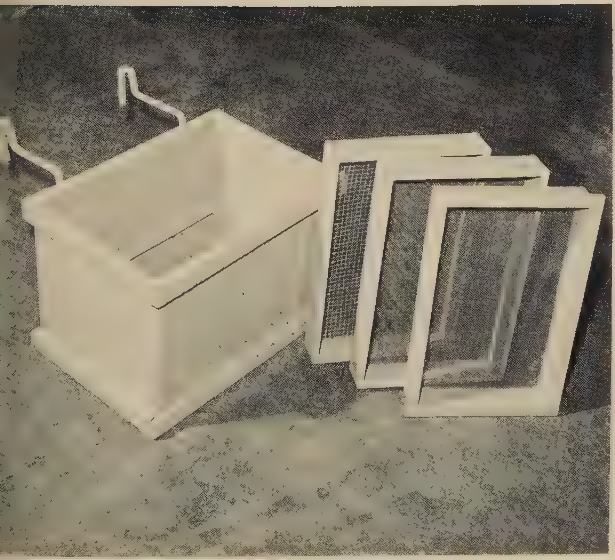

Figure 5.—Screen box and three nesting screens used to separate organisms from bottom sediments.

The *Syndosmya-Alba* community described by Petersen and Jensen from Danish waters (see review by Thorson 1957, p. 510) appears to be a close counterpart of the *Nephtys-Nucula* community. The original definition of the *Nephtys-Nucula* community and comparison with communities from other geographical areas can be found in Sanders (1956).

SUMMARY

A *Nephtys-Nucula* community is described from a series of bottom samples taken with a Petersen-type grab. The community was found in areas of the Sheepscot River estuary and has been previously described from similar soft mud sediments in Buzzards Bay, Mass., and Long Island

Sound. The faunal composition of the community is similar in all areas but incidental species composition varies with geographical location. *Nucula proxima*, a pelecypod, and *Nephtys incisa*, a polychaete, are the dominant organisms of the Sheepscot community with cumaceans, a hemichordate, a pelecypod (*Thyasira gouldi*), and an amphipod (*Phoxocephalus holbolli*) also numerous and widely distributed.

The community is composed of small animals that inhabit the surface layers of the bottom sediment. They are mostly deposit or filter feeders. Their small size may be of advantage in competition with larger animals, at least in this environmental situation.

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H. L. Sanders and R. L. Wigley reviewed the manuscript.

LITERATURE CITED

Allee, Warder C.
1934. Concerning the organization of marine coastal communities. Ecological Monographs, vol. 4, pp. 541–554.

Bryant, Floyd G.
1956. Stream surveys of the Sheepscot and Ducktrap river systems in Maine. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 195, 19 pp.

Cowles, R. P.
1930. A biological study of the offshore waters of Chesapeake Bay. Bulletin of the U.S. Bureau of Fisheries, vol. 46, pp. 277–381.

Dexter, Ralph W.
1944. The bottom community of Ipswich Bay, Massachusetts. Ecology, vol. 25, No. 3, pp. 352–359.
1947. The marine communities of a tidal inlet at Cape Ann, Massachusetts: a study in bio-ecology. Ecological Monographs, vol. 17, pp. 261–294.

Hartman, Olga.
1955. Quantitative survey of the benthos of San Pedro Basin, Southern California. Part I, preliminary results. Allen Hancock Pacific Expeditions, vol. 19, No. 1, 185 pp.

Jones, N. S.
1950. Marine bottom communities. Biological Review (Cambridge Philosophical Review), vol. 25, No. 3, pp. 283–313.

Kingsley, J. S.
1901. Preliminary catalog of the marine invertebrata of Casco Bay, Maine. Proceedings of the Portland Society of Natural History [Portland, Maine] vol. 2, pp. 159–183.

Kirsop, F. M.
1922. Preliminary study of methods of examining the life of the sea bottom. Publications of the Puget Sound Marine (Biological) Station of the University of Washington, vol. 3, pp. 129–139.

Lee, Richard E.
1944. A quantitative survey of the invertebrate bottom fauna in Menemsha Bight. Biological Bulletin, vol. 86, No. 2, pp. 83–97.

Parker, Robert H.
1956. Macro-invertebrate assemblages as indicators of sedimentary environments in East Mississippi Delta region. Bulletin of the American Association of Petroleum Geologists, vol. 40, No. 2, pp. 295–376.
1959. Macro-invertebrate assemblages of central Texas coastal bays and Laguna Madre. Bulletin of the American Association of Petroleum Geologists, vol. 43, No. 9, pp. 2100–2166.
1960. Ecology and distributional patterns of marine macro-invertebrates, Northern Gulf of Mexico. Recent Sediments, Northwest Gulf of Mexico, 1951–1958. [Published by the American Association of Petroleum Geologists, Tulsa, Oklahoma] pp. 302–337, 368–381.

Petersen, C. G. Johan, and P. Boysen-Jensen.
1911. The valuation of the sea, Part I. Animal life of the sea bottom; its food and quantity. Report of the Danish Biological Station, vol. 20, 81 pp.

Petersen, C. G. Johan.
1913. The valuation of the sea, Part II. The animal communities of the sea bottom and their importance for marine zoogeography. Report of the Danish Biological Station, vol. 21, 44 pp.

Sanders, Howard L.
1956. Oceanography of Long Island Sound, 1952–1954. X. Biology of marine bottom communities. Bulletin Bingham Oceanographic Collection. [Peabody Museum of Natural History, Yale University], vol. 25, pp. 345–414.
1958. Benthic studies in Buzzards Bay. I. Animal sediment relationships. Limnology and Oceanography, vol. 3, No. 3, pp. 245–258.
1960. Benthic studies in Buzzards Bay. III. The structure of the soft bottom community. Limnology and Oceanography, vol. 5, No. 2, pp. 138–153.

helford, Victor E., Asa O. Weese, Lucile A. Rice, Daniel I. Rasmussen, N. M. Wismer, and J. H. Swanson.

1935. Some marine biotic communities of the Pacific coast of North America. Ecological Monographs, vol. 5, pp. 249–354.

oil Survey Staff.

1951. Soil survey manual. U.S. Department of Agriculture, Handbook 18. Government Printing Office, Washington, D.C., 503 pp.

tickney, Alden P.

1959. Ecology of the Sheepscot River estuary. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 309, 21 pp.

Stickney, Alden P., and Louis D. Stringer.

1957. A study of the invertebrate bottom fauna of Greenwich Bay, Rhode Island. Ecology, vol. 38, No. 1, pp. 111–122.

Sumner, Francis B., Raymond C. Osburn, and Leon J. Cole.

1913. A biological survey of the waters of Woods Hole and vicinity. Bulletin of the U.S. Bureau of Fisheries, vol. 31 (1911) [In two parts] pp. 1–544, 545–860.

Thorson, Gunnar.

1951. Animal communities of the level sea bottom. Annee Biologique, vol. 27, No. 7, pp. 249–257.

1956. Marine level-bottom communities of recent seas, their temperature adaptation and their "balance" between predators and food animals. Transactions of the New York Academy of Science, Section II, vol. 18, No. 8, pp. 693–700.

1957. Bottom communities (sublittoral or shallow shelf). *In* Treatise on Marine Ecology and Paleoecology. Geological Society of America, Memoir 67, vol. 1, pp. 461–534.

Verrill, A. E.

1873. Report on the invertebrate animals of Vineyard Sound and the adjacent waters. Report U.S. Fish Commission for 1871-1872, pp. 295–778.

Wieser, Wolfgang.

1960. Benthic studies in Buzzards Bay. II. The meiofauna. Limnology and Oceanography, vol. 5, No. 2, pp. 121–137.

Wigley, Roland L.

1956. Food habits of Georges Bank haddock. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 165, 26 pp.

UPWELLING IN THE COSTA RICA DOME

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ABSTRACT

The Costa Rica Dome is an area off the coast of Costa Rica where the strong tropical thermocline reaches to within 10 meters of the sea surface. The dome measures about 150 by 300 kilometers. It is situated near lat. 9° N., long. 89° W., at the eastern end of a ridge in the topography of the thermocline along the northern boundary of the Equatorial Countercurrent. This current, the Costa Rica Coastal Current, and parts of the North Equatorial Current form a cyclonic circulation around the dome.

At the surface the dome appears as an area of slightly reduced temperature, higher salinity and phosphate contents, and reduced oxygen saturation, which are indications of upwelling. The balance between the energy available for heating of the surface layer and the ascending of cooler water gives an average ascending velocity of 10^{-4} cm/sec. These movements add only 7×10^{10} cm.^{3}/sec. to the surface layer, compared with transports of about 20×10^{12} cm.^{3}/sec. of the horizontal circulation. The upwelling in the dome is caused by the cyclonic flow around the dome. When the Countercurrent strongly changes direction, the necessary adjustment of its velocity requires a cross-current velocity of about 0.9 cm./sec. which is sufficient to maintain the upwelling. During the Costa Rica Dome survey a deep-reaching eddy transporting 20×10^{12} cm.^{3}/sec. appeared to be separated and to drift north with the Costa Rica Coastal Current.

Comparison of the topography of an isothermal layer during six surveys in the area showed that the dome was always present and maintained its position within 200 km. These observations indicate that the Costa Rica Dome, although a permanent feature, is subject to considerable fluctuations in its structure and circulation and may contribute essentially to large-scale mixing.

The eastern tropical Pacific Ocean is characterized by a very well-developed thermocline separating the warm surface water from the cooler subsurface water. The warm surface layer is comparatively shallow, and the topography of the thermocline is related to the currents in the surface layer as shown by Cromwell (1958). The divergences and convergences associated with the surface circulation, which result in the formation of ridges and troughs in the topography of the thermocline, have particular importance for the fertilization of the surface layer and for the distribution of the standing crop of zooplankton in the area, as shown by Brandhorst (1958) and Reid (1962). A feature of special interest in this connection is the Costa Rica Dome in which the top of the thermocline often comes to within less than 10 m. of the surface. This dome is situated off the coast of Costa Rica at about lat. 9° N. and long. 89° W. and has a diameter of approximately 200 km.

As pointed out to me by Milner B. Schaefer, the Costa Rica Dome was found in 1948, when bathythermograph (BT) observations from vessels en route between California and Panama were examined. Between 1952 and 1958 a number of expeditions crossed or partly surveyed this dome, and confirmed its existence and approximate posi-

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[1] Contribution from Scripps Institution of Oceanography, New Series.

tion. However, none of these expeditions succeeded in covering the area of the dome sufficiently to allow a detailed analysis. As a consequence of this, a survey of the Costa Rica Dome was undertaken in November and December 1959 under the leadership of M. J. Pollak and E. B. Bennett of the Inter-American Tropical Tuna Commission (Scripps Institution of Oceanography, 1960). The results of this survey, which covered the dome as well as the surrounding area, are used in this paper to analyze the structure of the dome and draw conclusions about its role in the circulation of the eastern tropical Pacific Ocean, except where other expeditions are mentioned.

The objectives of this expedition were to locate the position of the dome properly, to determine its extent, and to study its circulation and its effects on the distribution of biota. Upwelling is thought to occur near the center of the dome, and an analysis of the data of the expedition should give an estimate of its amount and an indication of the sources of the ascending water, as well as an explanation of the upwelling from dynamic principles. From the point of view of physical oceanography, the questions to be discussed in this paper are the following:

i. Where is the upwelling area located, and what is its size?

ii. What is the amount of upwelling?

iii. Where does the ascending water come from?

iv. How is the upwelling conditioned dynamically?

v. Is the Costa Rica Dome a permanent or temporary feature?

These questions have a bearing upon the study of the tuna resources of the eastern tropical Pacific, which are exploited by United States fishermen. It could be expected that the spatial and temporal distribution of tuna would bear some relation to the distribution of upwelling, which, therefore, warrants investigation.

HYDROGRAPHIC STRUCTURE OF THE COSTA RICA DOME

The Costa Rica Dome appears as an area where the homogeneous surface layer is extremely thin and the top of the thermocline often comes to within less than 10 m. of the sea surface. Also, the thermocline itself is more strongly developed than in surrounding waters and temperature gradients usually exceed 1° C. per meter in the range between 25° and 17°. As a consequence of this, the cooler subsurface water is found in a higher position than in the surrounding area. These conditions are shown in figure 1 where the topography of the 24° isotherm, as derived from BT–observations, is drawn, as are two BT–sections across the dome. The 24° isotherm, which coincides fairly well with the top of the thermocline in this region, ascends to less than 10 m. depth in several patches within an area of approximately 350×150 km. On the periphery of the surveyed area this isotherm is found in depths of more than 20 m., its deepest positions being in the southeast. A BT–section (A–A) running from northwest to southeast and drawn from the same data is shown in the upper part of figure 1. The dome is situated between stations 7 and 11 where the thermocline is highest and the temperature gradient is steepest, and also where the cooler subsurface water of 13° reaches its highest position, ascending to less than 90 m. depth. This section does not cut through the shallowest parts of the dome but runs between the two patches in which the top of the thermocline is highest. In the northwestern part of the section another area with a high position of the thermocline is found, but there are not enough observations to relate this feature to the Costa Rica Dome.

A much more satisfactory BT–section (B–B) across the dome was obtained in February 1960 by the vessel *Explorer* (Stewart, 1962). This section is drawn in the lower part of figure 1 and shows that the dome is situated between stations 331 and 369 in approximately the same position as during the Costa Rica Dome survey, with a diameter of about 230 km. The two sections run in the same general direction from northwest to southeast, but there is no shallow thermocline in the northwestern part of the *Explorer* section. Therefore, the shallow thermocline observed during the Costa Rica Dome survey in the northwest may be considered as a transient feature.

At the surface the dome appears as an area of slightly lower temperature, slightly higher salinity, reduced percent of oxygen saturation, and high phosphate concentration, although the centers of the areas defined by these properties do not completely coincide (fig. 2). Temperature near the center of the dome exhibits a more irregular pattern than on its periphery, where it usually exceeds 27° C. Near the center, patches of water of less than 25° C. are found beside patches

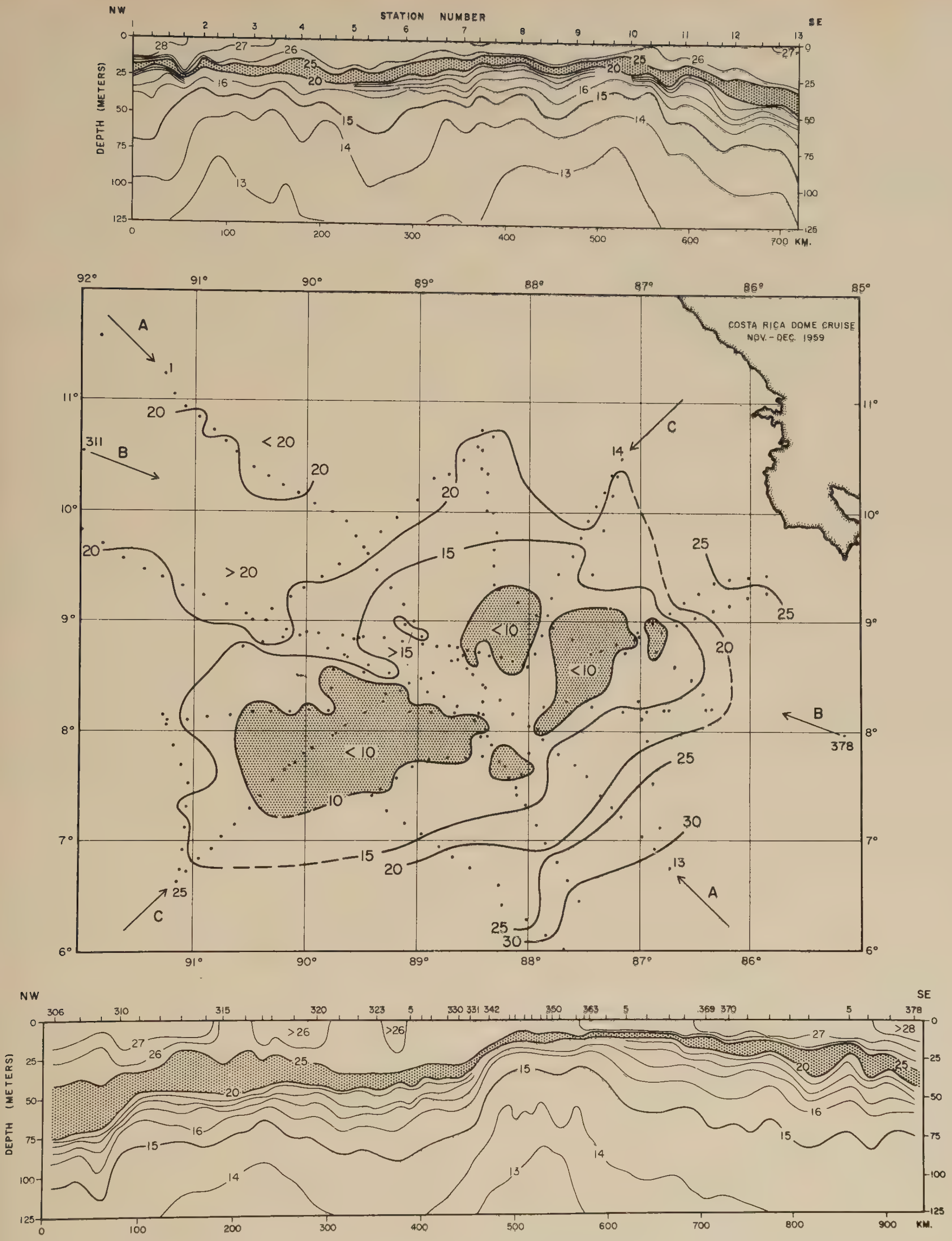
NW
STATION NUMBER
SE
DEPTH (METERS)
700 KM.
COSTA RICA DOME CRUISE
NOV.-DEC. 1959
A
B
C
< 20
> 20
>15
<10
311
378
NW
SE
DEPTH (METERS)
>26
>28
KM.

FIGURE 1.—The thermal structure of the Costa Rica Dome from bathythermograph observations. Center: Topography of the 24° C. isotherm during the Costa Rica Dome cruise, in meters, <10 m. shaded. Top: Distribution of temperature along section A–A during the Costa Rica Dome cruise; thermocline between 25° and 20° C. shaded. Bottom: Distribution of temperature across the dome in February 1960 according to observations of the vessel *Explorer* along section B–B; thermocline between 25° and 20° C. shaded.

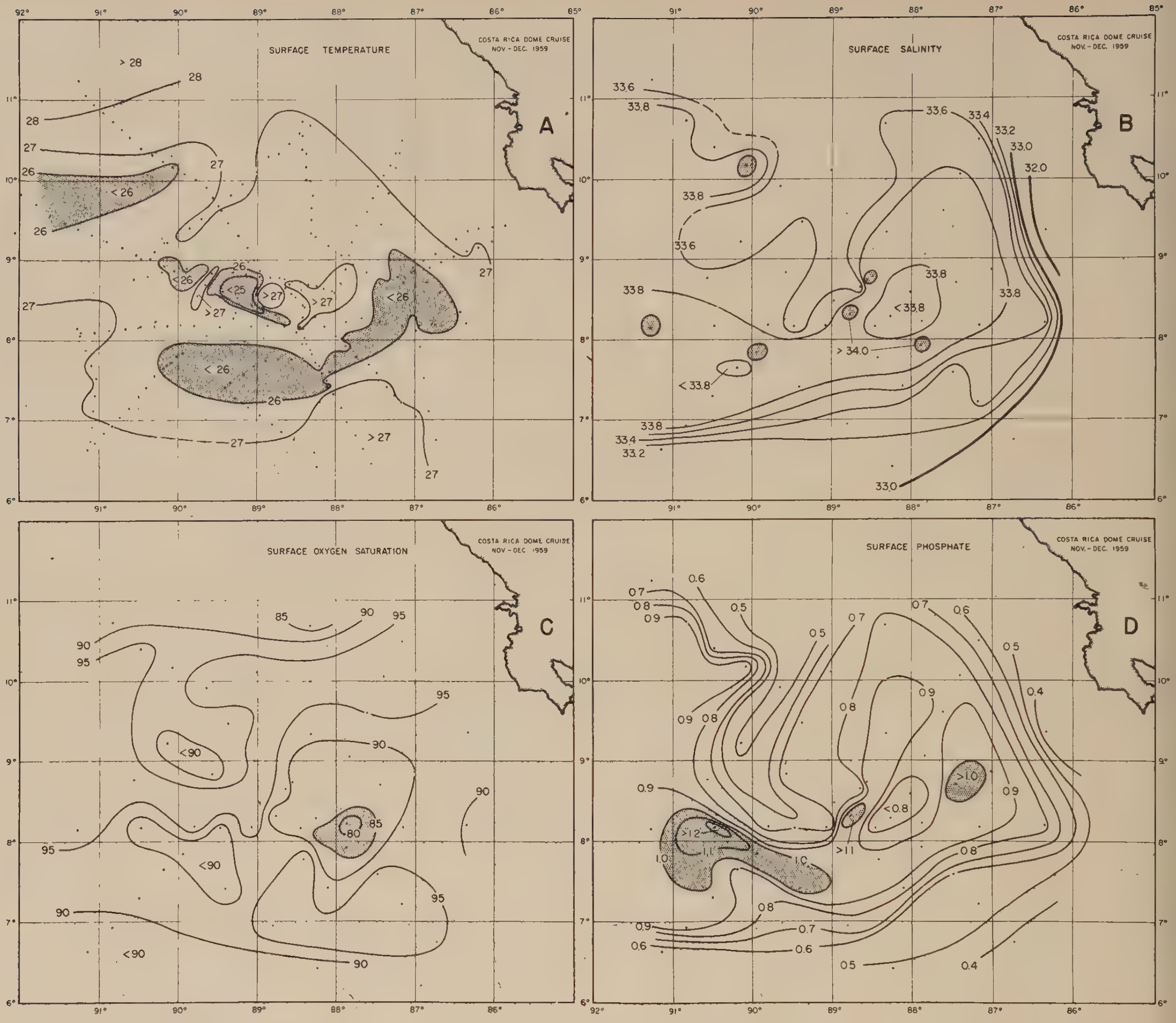
SURFACE TEMPERATURE
COSTA RICA DOME CRUISE NOV.-DEC. 1959
A
> 28
28
27
26
< 26
<25
>27
27
> 27
SURFACE SALINITY
COSTA RICA DOME CRUISE NOV.-DEC. 1959
B
33.6
33.8
33.4
33.2
33.0
32.0
<33.8
> 34.0
SURFACE OXYGEN SATURATION
COSTA RICA DOME CRUISE NOV.-DEC. 1959
C
85
90
95
<90
80
SURFACE PHOSPHATE
COSTA RICA DOME CRUISE NOV.-DEC. 1959
D
0.6
0.7
0.8
0.9
0.5
0.4
>1.0
<0.8
>1.2
1.1
1.0
>1.1
92°
91°
90°
89°
88°
87°
86°
85°
11°
10°
9°
8°
7°
6°

Figure 2.—Distribution of properties at the surface during the Costa Rica Dome cruise. (A) Surface temperature, $<26^{\circ}$ C. shaded. (B) Surface salinity, $>34.0^{\circ}/_{\circ\circ}$ shaded. (C) Percent of oxygen saturation at the surface, <85 percent shaded. (D) Surface phosphate-phosphorus, >1.0 µg.-atom/L. shaded.

with more than 27° C. (fig. 2A). This pattern indicates a patchiness of the actual upwelling, which occasionally and locally may bring the top of the thermocline right to the surface, but this is definitely an exception. The cooler water is situated between lat. 7.5° and 9° N. and between long. 87° and 90° W. Although the surface temperature shows a drop of as much as 2° C. in some places, it should be noted that during this survey no water within the temperature range of the thermocline reaches right to the surface and in all instances a shallow surface layer is shown in the BT-observations.

The distribution of surface salinity (fig. 2B) shows a tongue of high salinity extending eastwards between lat. 7° and 8° N. The salinity within this tongue is above $33.8^{\circ}/_{\circ\circ}$, and only in a few places is $34.0^{\circ}/_{\circ\circ}$ exceeded. East of long. 89° W. the tongue turns north and its salinity is reduced. It seems to reach about lat. 11° N. To the south and to the east a sharp salinity gradient separates the tongue from the water of low salinity ($<33^{\circ}/_{\circ\circ}$) off the coast of Central America. This salinity gradient is not accompanied by a corresponding change of surface temperature.

The surface water is undersaturated with oxygen n the entire area, values being between 88 and 98 percent (fig. 2C). In a small area near lat. 8° N., long. 88° W., oxygen saturation at the surface drops below 85 percent indicating an advection of subsurface water of low oxygen content into the shallow surface layer. The phosphate concentration at the surface is high; only in the range of the low salinity water off Central America are the phosphate values less than 0.6 μg.-atom/L. (fig. 2D). The distribution of the phosphate resembles closely that of surface salinity with a tongue of high phosphate coinciding with the tongue of high salinity. Within this tongue phosphate is in some places as high as 1.0–1.2 μg.-atom/L.

In the center of the tongue of water of high phosphate content, an area near long. 88° W. has phosphate values below 0.8 μg.-atom/L. This area coincides with an area of reduced salinity (<33.8‰) within the tongue of high salinity, and with an area where the surface temperature is above 27°. Because upwelling in the dome should be indicated by low temperature, high salinity, and high phosphate, this patch of abnormal water in the center of the dome suggests that circulation and upwelling in the dome must be subject to fluctuations that can lead to the isolation of a patch of water of this size. The lowest oxygen saturation is found just to the southeast of this patch of abnormal water.

According to this analysis of the topography of the thermocline and of the distribution of properties at the surface, the Costa Rica Dome appears as the end of a ridge in which the thermocline is in a very shallow position. This ridge extends along the left or northern flank of the Equatorial Countercurrent, as shown by Cromwell (1958). When this current approaches the coast of Central America and turns north, the ridge is abruptly terminated, and the Costa Rica Dome is at its end. In this dome the thermocline comes even closer to the surface than is the case along the ridge at the northern boundary of the Countercurrent, indicating that upwelling occurs in the dome area. The dome was situated between lat. 7.5° and 9° N. and between long. 87° and 90° W. during this survey.

Within the strong tropical discontinuity layer, temperature decreases rapidly from about 25° to 15° C. within a depth interval of only 20 to 50 m., and the other properties also change considerably. Salinity and phosphate content increase while oxygen content decreases, as shown by the distribution of these properties between the surface and 800 m. depth along a section crossing the dome area from southwest to northeast (fig. 3). This is section C–C in figure 1. Below 15° C. the

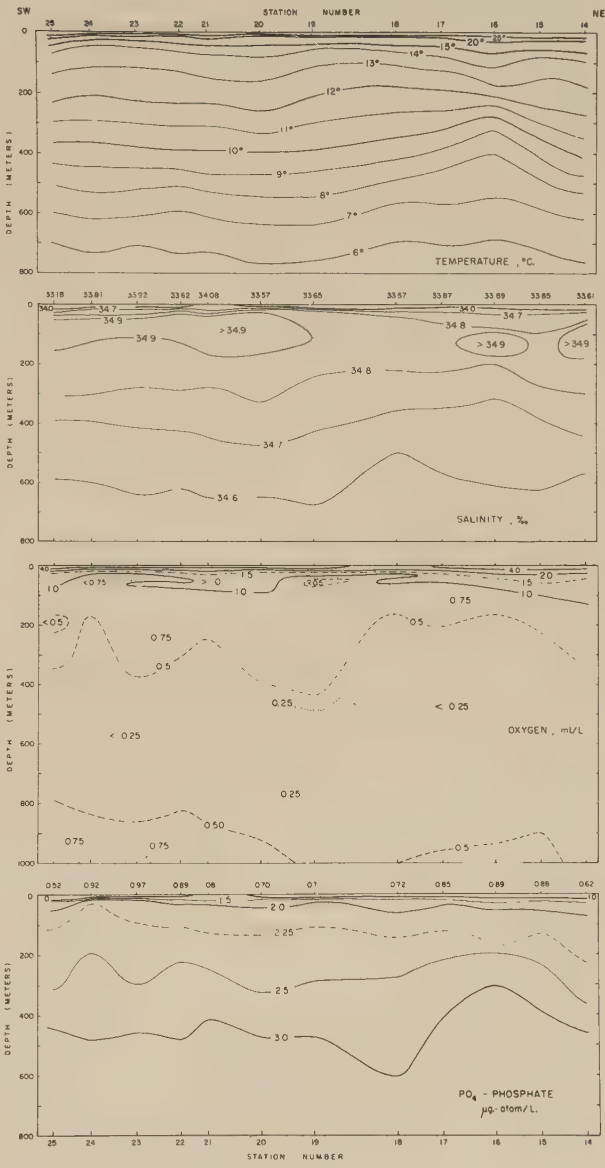

FIGURE 3.—Distribution of temperature, salinity, oxygen content (ml./L.), and phosphate-phosphorus between the surface and 800 m. depth along a section from southwest to northeast across the Costa Rica Dome, on the Costa Rica Dome cruise. The position of the section is shown in figure 1 by the line C–C.

temperature decrease is much slower and the salinity reaches a maximum near 100 m. depth in which salinities are close to 34.9°/oo. In the layer between 50 and 300 m. depth the oxygen content shows a number of maxima and minima before decreasing to values of less than 0.25 ml./L. and reaching the main oxygen minimum. These intermediate oxygen maxima and minima do not exhibit any uniformity with respect to the depth and temperature at which they are found. It is likely that this irregular oxygen distribution results from the local variability of the quantity and activity of oxygen-consuming material, as well as from the horizontal advection of smaller water bodies of higher oxygen content. The main oxygen minimum is found in depths between 400 and 700 m. in which oxygen content is everywhere lower than 0.20 ml./L. Below this layer oxygen increases again and the salinity reaches a minimum near 1,000 m. with salinities below 34.6°/oo which are characteristic for the Intermediate Water. Phosphate, which is already unusually high at the surface, increases to 2.0 μg.-atom/L. at about 50 m. and then much more slowly to values above 3.0 μg.-atom/L. in the lower part of the oxygen minimum layer.

The vertical structure of the water masses in the area of the Costa Rica Dome is shown by the envelopes of all temperature-salinity and temperature-oxygen curves in figure 4. Below the surface layer of high temperature and comparatively low salinity, salinity increases to a maximum which is situated between 30 and 150 m. depth. The salinity in this salinity maximum is charted in figure 5a and varies only between 34.83 and 34.96°/oo. This subsurface salinity maximum is found everywhere in the eastern tropical Pacific Ocean and will be called the Equatorial Subsurface Water. A close analysis of the salinity maximum (not presented here) and of its depth shows that two branches are present in the area of the Costa Rica Dome. One branch is found east of long. 90° W. and the maximum is in depths between 80 and 150 m.; the other branch is found west of long. 88° W. and the maximum is between 30 and 60 m. depth. Between long. 88° and 90° W. the two maxima overlap and a double maximum is found. The salinities in the two branches are not different, and the small gradients seen in figure 5A do not allow one to draw conclusions about the spreading of the two branches. In the center of the dome, where the thermocline is highest, the salinity maximum is lowest and drops in some places below 34.85°/oo. This reduced salinity can be taken as an indication of upwelling in these localities because the ascending motion would tend to reduce the salinity in the maximum.

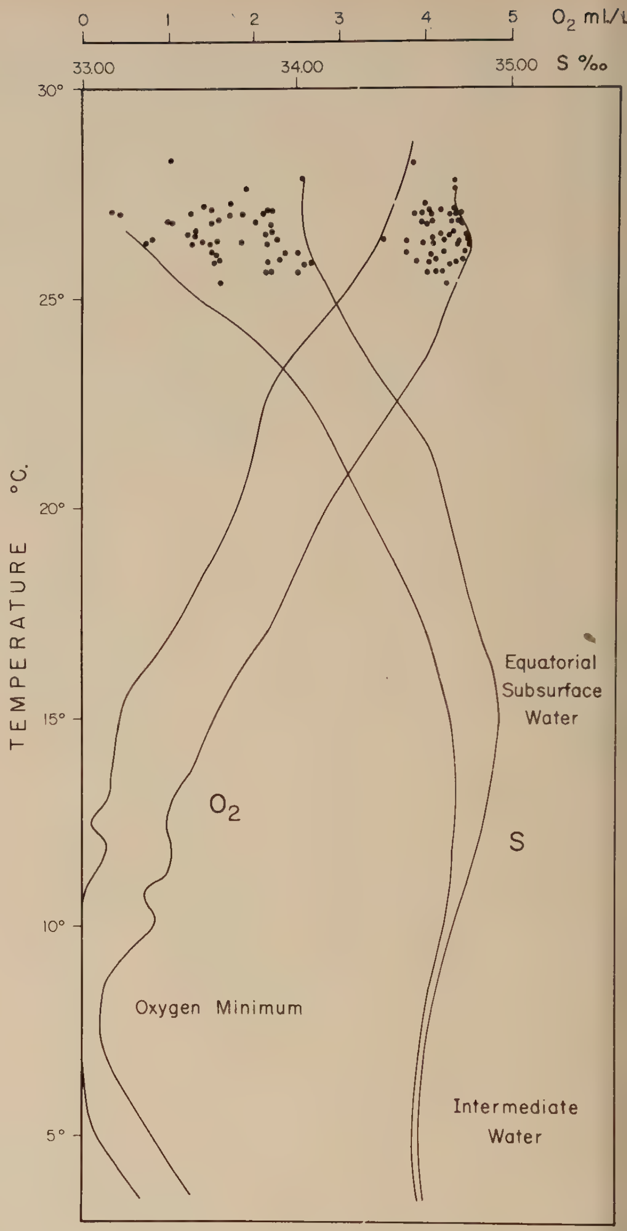

FIGURE 4.—Temperature-salinity and temperature-oxygen diagram showing the envelopes of all TS- and TO_2-curves during the Costa Rica Dome cruise. Surface values are entered by dots, and names of the main water masses are indicated.

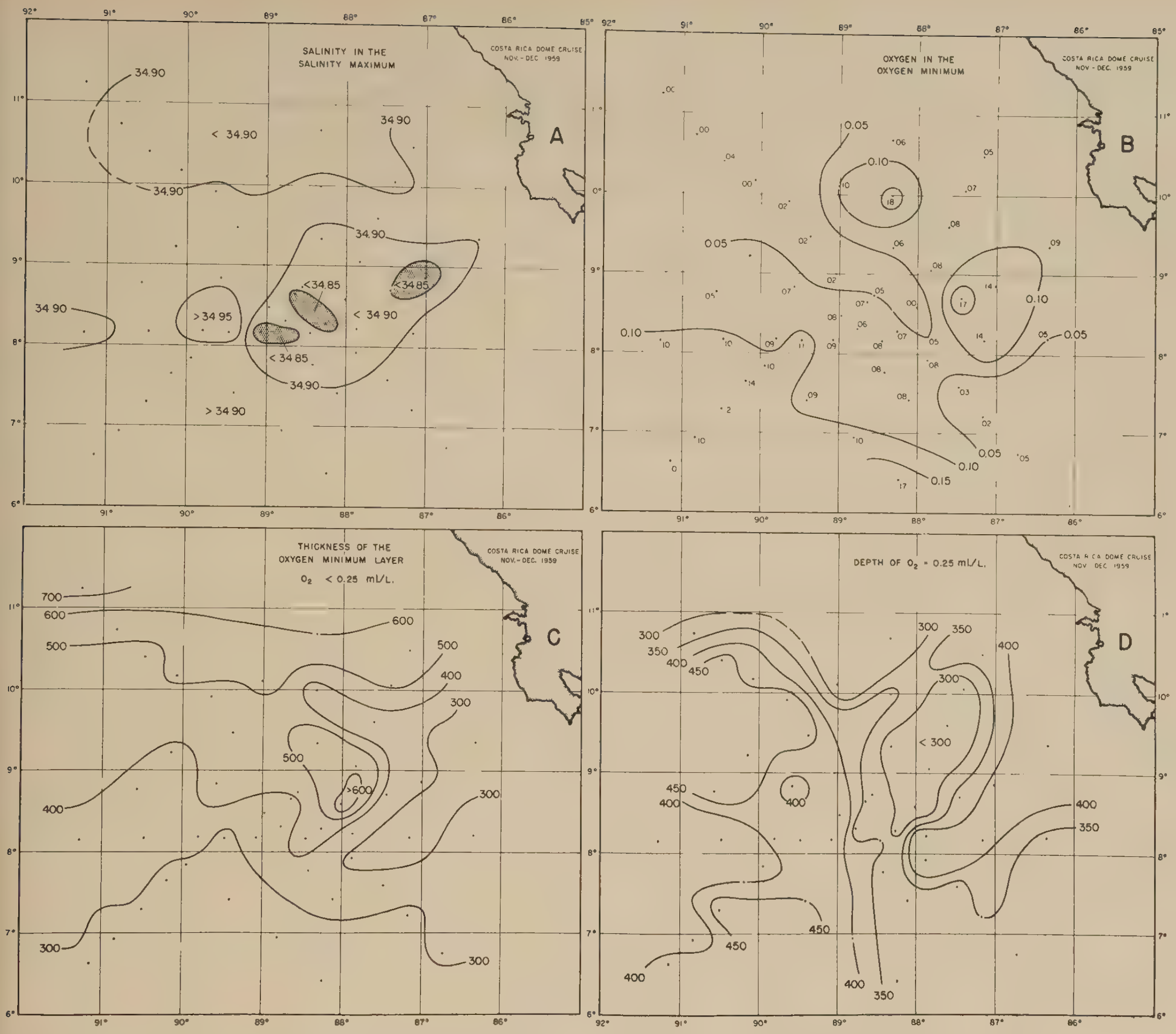
SALINITY IN THE SALINITY MAXIMUM
COSTA RICA DOME CRUISE NOV.-DEC. 1959
A
34.90
< 34.90
> 34 95
<34.85
< 34 90
> 34 90
OXYGEN IN THE OXYGEN MINIMUM
B
0.05
0.10
0.15
THICKNESS OF THE OXYGEN MINIMUM LAYER O₂ < 0.25 ml/L.
C
700
600
500
400
300
>600
DEPTH OF O₂ = 0.25 ml/L.
D
300
350
400
450
< 300
92°
91°
90°
89°
88°
87°
86°
85°
11°
10°
9°
8°
7°
6°

FIGURE 5.—(A) Distribution of salinity in the salinity maximum of the Equatorial Subsurface Water, <34.85°/oo shaded. (B) Minimal oxygen content in the oxygen minimum layer, in ml./L. Values at station positions are in 0.01 ml./L. (C) Thickness of the oxygen minimum layer (where 0_2 <0.25 ml./L.) in meters. (D) Depth of the upper boundary of the oxygen minimum layer, given by the depth of the 0.25 ml./L. surface in meters.

n the range of the Equatorial Subsurface Water, xygen content varies widely but is, in general, ow, between 2.0 and 0.25 ml./L., and shows internediate maxima and minima.

In depths near 900 m. the Intermediate Water s found, characterized by a salinity minimum at , temperature of about 5° C. The salinities in he minimum are uniform and range only between 4.56 and 34.58°/oo in the entire area surveyed.

The main oxygen minimum is situated between he Equatorial Subsurface and the Intermediate Vater and extends over a considerable interval of depth. Oxygen concentrations in the minimum are everywhere in the area below 0.20 ml./L. (fig. 5B) and in some places they are close to zero. Because the oxygen content remains at this low level within a fairly thick layer, it is not possible to chart the depth of the minimum with confidence and it is advisable to chart instead, the thickness of the layer that has an oxygen content of less than 0.25 ml./L. (fig. 5C) and the upper limit of the oxygen minimum layer as given by the depth of an oxygen content of 0.25 ml./L. (fig. 5D). The thickness of the oxygen minimum layer increases from about 250 m. in the south to more than 600 m. in the north. Only underneath the dome, at lat. 9° N. and long. 88° W., is this regular increase in thickness interrupted and the oxygen minimum layer reaches a thickness of 600 m. in contrast to only 400 m. in the immediate vicinity. The upper limit of the oxygen minimum, as given by the depth where the oxygen content is 0.25 ml./L. shows a more irregular pattern. The highest position of this surface is found near lat. 9° N., and long. 88° W., considerably displaced relative to the position of the dome as indicated in the topography of the thermocline. This displacement will be discussed in detail when the dynamics of the system is treated. In the north of the area, the 0.25 ml./L. oxygen surface is also in a very high position but this is due to the great thickness of the oxygen minimum layer.

HORIZONTAL CIRCULATION

The Costa Rica Dome is north of the Equatorial Countercurrent. This current approaches the coast of Central America between lat. 4° and 8° N. during all seasons, with the exception of February and March when it seems to be absent or only weakly developed as shown in the surface current charts drawn by Cromwell and Bennett (1959). Along the coast of Costa Rica a coastal current flows northwest, separating the dome from the coast. It will be called the Costa Rica Coastal Current. This coastal current seems to carry away part of the water that is accumulated by the Countercurrent off the coast of Panama and Costa Rica. North of about lat. 10° N., the flow is to the west and the water movements are part of the system of the North Equatorial Current. The center of this cyclonic circulation off the coast of Costa Rica is the Costa Rica Dome as revealed from the topography of the thermocline.

The circulation in the vicinity of the Costa Rica Dome is shown in figure 6 by the topography of four surfaces relative to 1,000 decibars. The topography of the sea surface (fig. 6A) shows a strong current entering the region from the west and southwest turning north and later, northwest. The right flank of this current coincides with the strong salinity gradient seen in the chart of surface salinity (fig. 2B). This flow represents the northern part of the Equatorial Countercurrent which is south of lat. 7° N. when entering the area at long. 91° W. East of long. 89° W. parts of the Countercurrent turn northeast and pass over into the Costa Rica Coastal Current. This map does not show how close this current reaches to the coast because the easternmost station is almost 100 km. offshore. In the northwestern part of the area the flow is from the north but turns west before reaching lat. 8° N. To the west of the Costa Rica Coastal Current an eddy has its center near lat. 8.5° N., long. 88° W., but the closed circulation in this cyclonic eddy is small compared with the strength of the coastal current. Another part of a cyclonic circulation can be seen at lat. 7.5° N., long. 91° W., where some water from the Countercurrent turns north and passes over into a flow to the west.

The circulation at 50 m. depth (fig. 6B) has substantially decreased in intensity as compared with the surface circulation. The Equatorial Countercurrent has lost in strength or may be found farther south. Also, the coastal current is weaker. However, the closed circulation in the eddy, whose center has shifted to about lat. 10° N., long. 88° W., has increased. This change in the circulation between the surface and 50 m. depth reflects the influence of the strong discontinuity layer situated between about 10 and 50 m. depth. The topography of the 100-decibar surface is almost identical to that of the 50-decibar surface if 10 dynamic centimeters are subtracted, so this chart is not shown.

The circulation at 200 m. depth (fig. 6C) is completely dominated by the huge eddy which is now centered near lat. 10° N., long. 88° W. The only other feature worth mentioning is the cyclonic circulation around a point near lat. 8° N., long. 91° W., which was already indicated in the topography of the sea surface. Below 300 m. depth velocities in the eddy decrease progressively, but even in depths near 700 m. this eddy is still shown in charts of the topography of isothermal layers. Thus, for instance, the 6° isotherm rises to less than 680 m. in the center of the eddy compared to more than 750 m. at its periphery, but the map is not shown here.

The vertical distribution of velocity and the transports across some sections are shown in figure 7 and the positions of the sections are

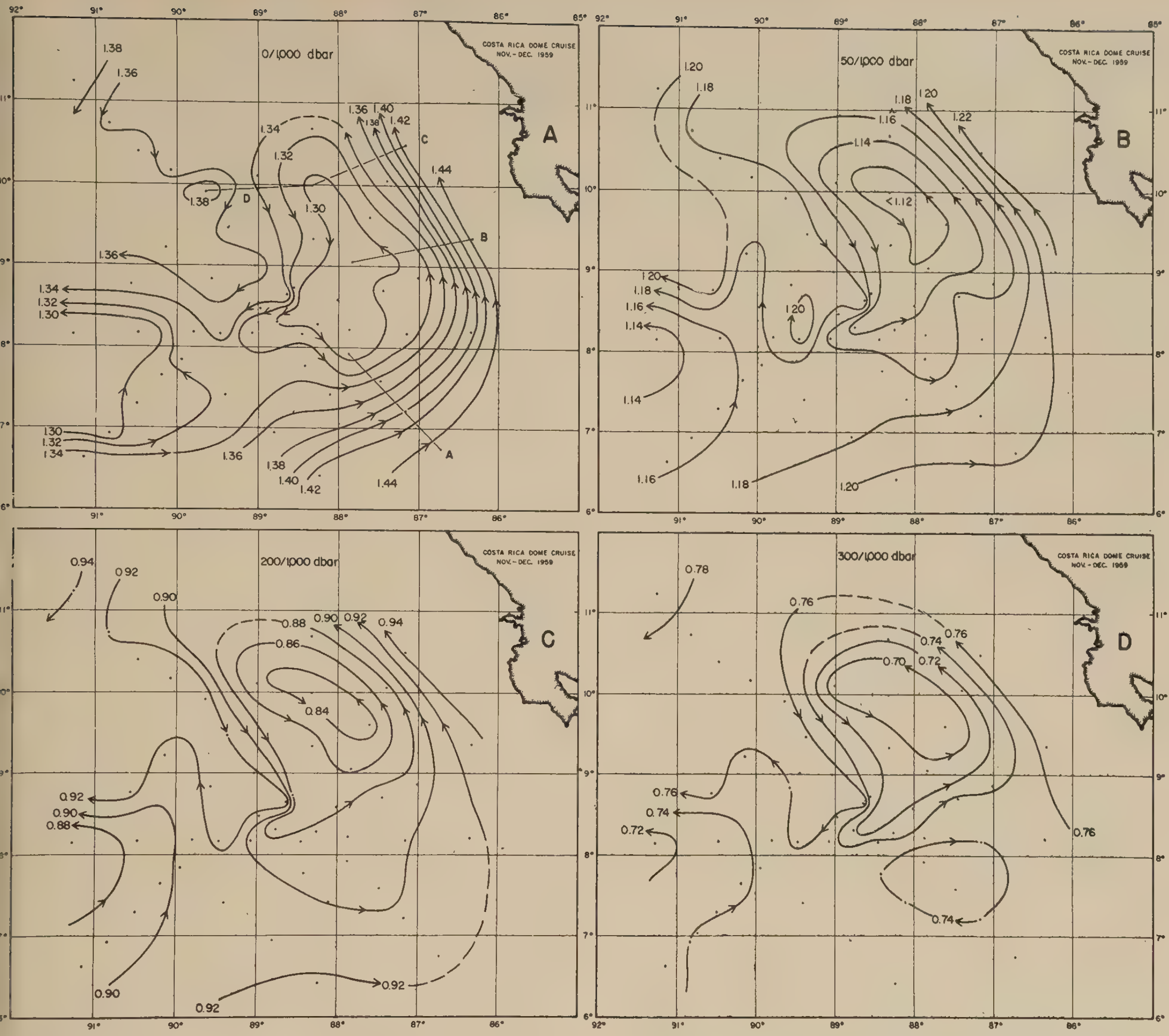
0/1,000 dbar
50/1,000 dbar
200/1,000 dbar
300/1,000 dbar
COSTA RICA DOME CRUISE NOV.-DEC. 1959
A
B
C
D
92°
91°
90°
89°
88°
87°
86°
85°
11°
10°
9°
8°
7°
6°
1.38
1.36
1.34
1.32
1.30
1.40
1.42
1.44
1.20
1.18
1.16
1.14
1.22
<1.12
0.94
0.92
0.90
0.88
0.86
0.84
0.78
0.76
0.74
0.72
0.70

FIGURE 6.—Geopotential topographies of the sea surface, and of the 50-, 200-, and 300-decibar surfaces relative to 1,000 decibars during Costa Rica Dome cruise, in dynamic meters. The positions of sections for which transports have been calculated are marked in figure 6A by the lines A, B, C, and D.

ndicated in figure 6A. Section A, between tations 10 and 13, crosses the Countercurrent ust before it turns north. The average velocity t the surface is 43 cm./sec., but velocities of more han twice this value have been observed near he center of the current by surface drogues. 'he velocity decreases rapidly with depth and he total transport of 7.2 million m.^{3}/sec. between hese two stations is chiefly concentrated in the pper 150 m. From the topographies of the ubsurface layers it can, however, be seen that his section does not include the transport in the east-going branch of the eddy in subsurface layers because station 10 is situated to the south of this flow. Section B, which cuts across the north-flowing part of the eddy, still shows a thin surface layer moving more rapidly than the subsurface layer, but most of the transport of 16.7 million m.^{3}/sec. is due to the flow in layers between 50 and 400 m. depth. Sections C and D have each a transport of about 20 million m.^{3}/sec. flowing north and south, respectively. These transports are concentrated between the surface and 400 m. depth, and the velocities are almost uniform from the surface to that depth, especially in section D.

The circulation pattern in this area is characterized by the Equatorial Countercurrent flowing eastwards in the southern part of the area and by parts of the North Equatorial Current flowing west in the northern part of the area. Along the coast the northward flowing Costa Rica Coastal Current transfers water from the Countercurrent, which accumulates water off the coast, to the North Equatorial Current. A trough in the topography of the sea surface and a ridge in the topography of the discontinuity layer are developed between the flow to the east and the flow to the west. This trough is terminated by the north-flowing coastal current and does not reach the coast. The ridge in the topography of the thermocline is simultaneously terminated. The Costa Rica Dome is the very pronounced end of this ridge that separates the Equatorial Countercurrent from the North Equatorial Current. Around the eastern end of this ridge there is a strong cyclonic circulation.

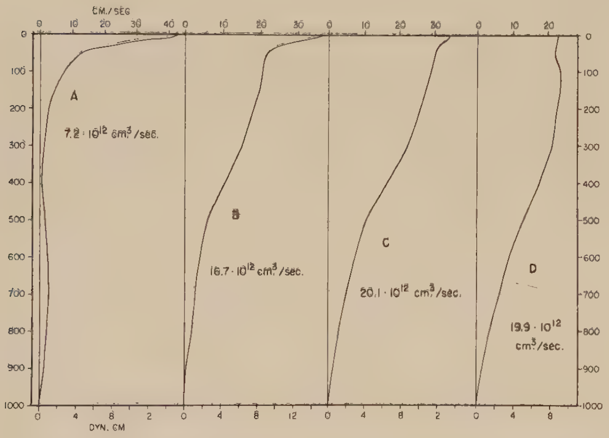

Figure 7.—Vertical distribution of the average geostrophic velocity (cm./sec.) relative to 1,000 m. depth in different branches of the circulation in the Costa Rica Dome. (The sections for which the transports have been calculated are shown by A, B, C, and D in figure 6A.)

Although this general picture of the circulation seems to be quite simple, there are some problems and observed features requiring an explanation. The flow in the North Equatorial Current, as well as the flow in the countercurrent, were comparatively weak and shallow during this survey, and this is generally the case, as can be seen from surface current charts. Therefore, it is not obvious how these currents can maintain an eddy of considerable depth with a circular transport of the order of 20 million m.^{3}/sec. If this eddy should be a stationary feature, it would require additional energy for its maintenance. Winds in this region, however, are weak and variable in direction, so that they cannot really be considered as a source of energy for such a strong, limited eddy. Moreover, there is little vertical shear in the eddy, as demonstrated by the weak velocity gradients between 50 and 300 m. depth in the eddy (fig. 7). Since there is no obvious source of energy to supply a stationary eddy in this position, the eddy may be considered as transient and the motion around the Costa Rica Dome as nonstationary. This assumption is partly supported by the fact that the center of the eddy in subsurface layers (fig. 6B, C, D) does not coincide with the center of the Costa Rica Dome (fig. 1) which is the area where the highest thermocline is.

To solve this problem, it should be investigated whether a similar eddy was found during other surveys of the same region. During the Eastropic Expedition in November 1955 (Scripps Institution of Oceanography, 1956) the area of the Costa Rica Dome was also surveyed although the station network was less dense. The data from that survey were used to plot the distribution of surface salinity and the topography of the sea surface relative to 1,000 decibars (fig. 8) for comparison with the situation during the Costa Rica Dome cruise. The difference is quite obvious. There is again a cyclonic circulation around a point at lat. 9° N., long. 89.5° W., but there is no separate eddy, at least not east of long. 90° W. The water entering the area with the Equatorial Countercurrent turns north, and later, northwest, but nowhere is a flow to the south indicated as in figure 6a. The center of the cyclonic flow coincides with an area of lowest surface temperature ($<25°$ C., fig. 8B) and highest surface salinity ($>33.8‰$, fig. 8A). The low salinity water of the Costa Rica Coastal Current occupies a larger area but is displaced to the northwest.

From this comparison it may be concluded that the cyclonic circulation around the eastern end of

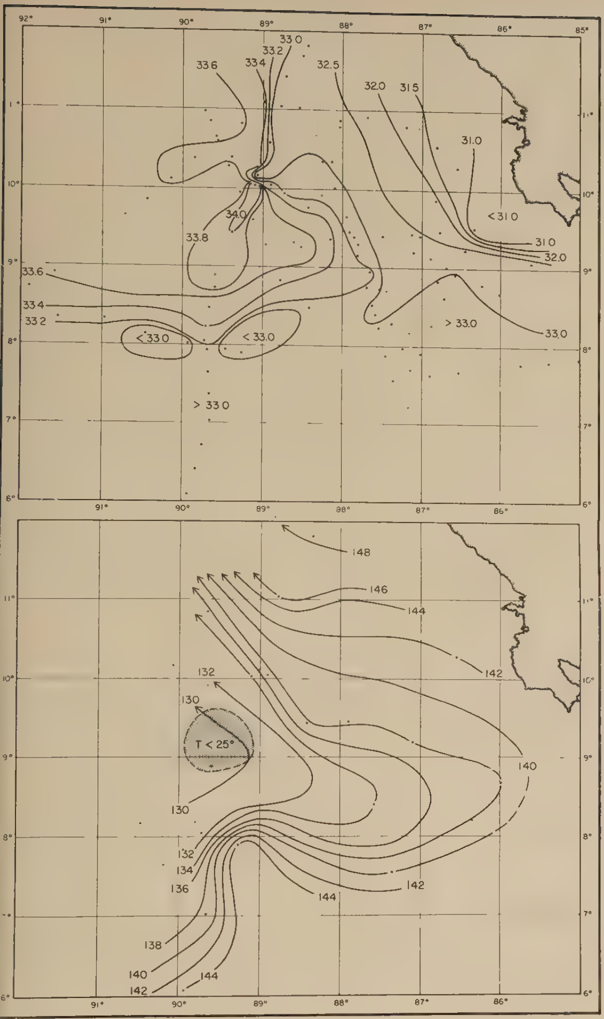

FIGURE 8.—A. Surface salinity (°/₀₀) during Eastropic Expedition. B. Geopotential topography of the sea surface relative to 1,000 decibars during Eastropic Expedition, in dynamic cm. (The area with surface temperatures below 25° C. is shaded.)

the trough separating the Countercurrent from the North Equatorial Current is not very stable and separates eddies from time to time. One of these eddies has been met during the Costa Rica Dome survey. This eddy seems to drift north or northwest on the left flank of the Costa Rica Coastal Current, as indicated by the displacement of its center towards the northwest, relative to the center of the dome. The reasons for the separation of such eddies are probably fluctuations in the strength and transports of the Countercurrent. Knauss (1961) has reported fluctuations in the transport of the Countercurrent by as much as an order of magnitude, and it can be assumed that as a result of each of these major fluctuations one big eddy will be separated near the Costa Rica Dome where the Countercurrent ends. This eddy is similar in size to an eddy separate from the Gulf Stream which was observed by Fuglister and Worthington (1951).

The other feature to be explained is the different position of the center of the deep eddy and that of the thermal dome during the Costa Rica Dome cruise. Such a separation did not occur during the Eastropic Expedition when the lowest surface temperatures and the highest surface salinities coincided with the center of the cyclonic circulation (fig. 8). During the Costa Rica Dome survey, on the other hand, the center of the deep eddy was found near lat. 10° N., long. 88° W., while the thermal dome was situated between lat. 7.5° and long. 9° N. and between lat. 90.5° and long. 87° W. The discussion of the geopotential topographies mentioned that the circulation above the thermocline was substantially different from that at 50 m. depth, thus indicating the presence of a fairly independent surface layer. This finding leads to the conclusion that the thermal dome is related to the circulation within the thin surface layer and little or not at all influenced by the circulation in deeper levels. This conclusion will be substantiated in the next section.

The structure of the deep eddy, as well as the fact that the dome is developed in a different position, indicates that this eddy is already separated from the remainder of the circulation. This is also emphasized by the development of another cyclonic circulation near lat. 8° N., long. 91° W., where parts of the Countercurrent turn north and west into the North Equatorial Current (fig. 6). This cyclonic circulation is probably the start to re-establish the old circulation after the separated eddy in the northeast has decayed and disappeared.

UPWELLING

The structure of the thermocline, which comes to within a few meters of the sea surface, the lowered surface temperature, and the higher salinity and phosphate content are clear indications of upwelling in the Costa Rica Dome. The ascending movements bring water out of the range of the thermocline into the thin suface layer in which it is removed horizontally. This continuous addition of cooler water from beneath requires that the ascending water be heated in order to maintain the temperature in the surface layer. The fact that the top of the thermocline does not reach to the surface but is, perhaps with occasional local exceptions, always covered by a thin surface layer demonstrates that the circulation in the dome area is in thermal balance and, therefore, the maximal possible ascending velocity is limited by the amount of energy available for the heating of the surface layer. In order to determine this maximal upwelling velocity a few calculations of the heat balance of the dome will be made in the following.

For the purpose of the calculations the dome will be considered as circular with the radius r. There will be a homogeneous surface layer of thickness D with the temperature T_o (fig. 9).

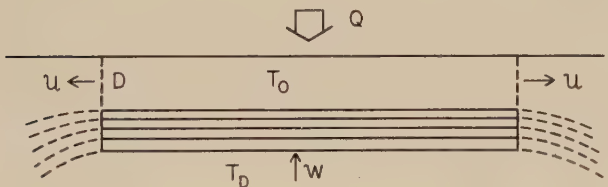

Figure 9.—Notations used for the calculation of the heat balance of the Costa Rica Dome.

Underneath this surface layer is the thermocline, and within this thermocline a constant ascending velocity w is assumed. The ascending water is assumed to come from the layer immediately beneath the thermocline out of a depth between 75 and 200 m. where the temperature is between 12° and 14° C. and the temperature gradient considerably weaker (figs. 1 and 3). This layer is assumed to form the reservoir for the ascending water, and its temperature is T_D. The water entering the surface layer from beneath is thought to flow horizontally away within the surface layer with the velocity u. The thermocline is assumed to be without horizontal motion. The water balance is then given by

$$2r\pi Du = r^2\pi w \qquad (1)$$

and the heat balance by

$$2r\pi DuT_o = r^2\pi wT_D + r^2\pi\frac{Q}{\rho c} \qquad (2)$$

where Q is the energy available for heating of the surface layer, ρ is the density, and c the specific heat of sea water. The energy available for heating the surface layer of the ocean results chiefly from the difference between incoming and outgoing radiation less the energy used for evaporation. Budyko (1956) has charted these quantities for the entire earth, and, according to his maps, about 110 cal.cm.$^{-2}$ day^{-1} are available for the heating of the surface layer in the region of the Costa Rica Dome. Because the annual variations in the terms of the heat balance in this area are small, it is satisfactory to use the estimate by Budyko for the period of the Costa Rica Dome cruise.

Combining equations (1) and (2) gives the simple relation

$$w(T_o - T_D) = \frac{Q}{\rho c} \qquad (3)$$

which is independent of the size r of the area. With $Q=1.27\times10^{-3}$ cal. cm.$^{-2}$ sec.$^{-1}$, $T_o=25°$ C. and $T_D=13°$ C. the ascending velocity within the thermocline is $w=10^{-4}$ cm./sec. which is equal to 8.6 cm./day or 2.6 m./month. A velocity of this order will not disturb the temperature structure in the dome but will maintain it. A much greater velocity will be needed if "outcropping" of the thermocline should occur, but this seems to be the exception in the Costa Rica Dome. The vertical velocity calculated above, however, represents an average value for the entire area and locally higher or lower values are possible. Also the vertical velocity does not give any information about the structure of upwelling, and it is not unlikely that the actual upwelling occurs in smaller patches, in which temperature anomalies disappear rapidly as a result of horizontal mixing.

The horizontal velocity at the periphery of the dome is given by $u=\frac{rw}{2D}$ and with a radius $r=1.5\times10^7$ cm.$=150$ km. the velocity is $u=0.38$ cm./sec. The total amount of upwelling in the dome is given by $T=wr^2\pi=7\times10^{10}$ cm.^{3}/sec. This is less than a tenth of a million $m.^3$/sec. and very small compared with the strength of the horizontal circulation.

Knowledge of the approximate value of the vertical velocity within the thermocline allows the calculation of the vertical exchange coefficient A within this strong tropical thermocline. The equation of the vertical diffusion of heat is given by

$$\frac{\partial T}{\partial t}=\frac{\partial}{\partial z}\left(wT-A\frac{\partial T}{\partial z}\right). \qquad (4)$$

If the thermocline is considered to be stationary $\left(\frac{\partial T}{\partial t}=0\right)$, the advection of cooler water from below must be compensated by a turbulent flow of heat from above. Taking w and A as a constant within the thermocline, equation (4) can easily be integrated

$$T=T_D+(T_o-T_D)e^{\frac{w}{A}z} \qquad (5)$$

where z has its origin at the top of the thermocline and is positive upwards. Taking $T_o=25°$ C., $T_D=13°$ C. and a temperature $T=15°$ C. at 25 m. below the top of the thermocline, as is observed, a value $w/A=7.2\times10^{-4}$ cm.$^{-1}$ results. With $w=10^{-4}$ cm./sec. it follows that $A=0.14$ cm.^{2} sec.$^{-1}$. This value is reasonably close to that calculated by Montgomery (1939), who finds a maximal value of $A=0.4$ cm.^{2} sec.$^{-1}$ for the equatorial Atlantic Ocean.

The downward flow of heat Q_v is given by

$$Q_v=\rho cA\frac{\partial T}{\partial z}=\rho c(T_o-T_D)we^{\frac{w}{A}z} \qquad (6)$$

and decreases exponentially with depth. At the top of the thermocline ($z=0$) this flow is given by

$$\rho cA\left(\frac{\partial T}{\partial z}\right)_o=\rho c(T_o-T_D)w=Q$$

being the same equation as (3), which was derived from considerations of the heat balance of the entire dome, and shows that all the heat available in the surface layer diffuses down and that the heating of the ascending water takes place within the thermocline. At 25 m. below the top of the thermocline this vertical flow of heat has decreased to 0.2×10^{-3} cal. cm.$^{-2}$ sec.$^{-1}$. Consequently, it can be stated that in areas with no upwelling, where such a downward flow of heat will not be opposed by ascending cooler water, either the layers below the thermocline will be heated, or, more likely, the thermocline will descend with time, as is usual in higher latitudes with summer heating.

With the application of these calculations, it follows from the observed temperative distribution that the upwelling in the Costa Rica Dome, at least in the climatological average, is in thermal balance. This thermal balance limits the average ascending velocity to approximately 10^{-4} cm./sec. The amount of upwelling is of the order of 7×10^{10} cm.^{3}/sec. The ascending water is supplied from a layer immediately beneath the strong thermocline. The lower values of salinity in the salinity maximum, discussed in the section on "Hydrographic structure", indicate that water from these depths is ascending. All these results show that the Costa Rica Dome is a very shallow feature and must be closely related to and caused by the surface circulation. This is also strongly suggested by the fact that the circulation is appreciably different at the surface and below 50 m. depth as shown in the section on "Horizontal circulation".

The balance equations for phosphate can be studied now that the vertical circulation has been estimated from the heat balance equation. This is done by replacing the temperature in equation (3) with phosphate concentration, and the right-hand side then becomes the phosphate consumption

$$w(P_D-P_o)=X$$

Taking $P_D=2.3$ μg.-atom/L. for the water ascending from the layer between 50 and 200 m. depth, $P_o=0.5$ μg.-atom/L. for the water flowing horizontally away from the dome, and $w=10^{-4}$ cm./sec. as calculated from the heat balance, the phosphate consumption becomes $X=155$ μg.-atom/m.^{2}/day. When this figure is converted into weight and a relation $P{:}C=1{:}41$ is used the phosphate consumption is equivalent to 196.8 mg. C/m.^{2}/day. Measurements of *in situ* organic production in the Costa Rica Dome give values between 160 and 440 mg. C/m.^{2}/day (Holmes, personal communication), which agree very well with the calculated value of phosphate supply to the surface layer.

As the upwelling in the Costa Rica Dome has been found to be a very shallow process, its dynamics must be closely related to the circulation in the surface layer. This upwelling is situated at the northern flank of the Countercurrent in a position where this current turns sharply to the north. It will be assumed that the Countercurrent is in geostrophic balance when it approaches the area from the west. When turning to the north, the current has to attain a different balance and it will be shown that the necessary adjustment results in upwelling along the left flank of the turning current.

Winds in this area are irregular and weak, and wind charts do not indicate a permanent feature in the wind field, with the overall dimensions of the Costa Rica Dome, that could locally be important for maintaining the upwelling in the dome. Therefore, an effect of the local wind on the circulation and the upwelling in the dome will not be considered in the following discussion.

To describe the motion, natural co-ordinates (s, n) will be used, ds being tangential, dn normal to a trajectory. V is the velocity along the trajectory, which in the stationary case is also a streamline. The equations of a stationary motion in this system are

$$V\frac{\partial V}{\partial s}=-\frac{1}{\rho}\frac{\partial p}{\partial s} \qquad (7)$$

$$KV^2+fV=-\frac{1}{\rho}\frac{\partial p}{\partial n} \qquad (8)$$

where f is the coriolis parameter depending on the latitude, p the pressure and ρ the density. $K=\frac{1}{R}$ is the curvature of the trajectory, R the radius of curvature, both are functions of s.

It will be assumed that the current, represented by its isobars, enters the area from the west, as shown in figure 10. At point N the current may gradually start to turn north and reach its strongest curvature at point M. West of point N the curvature of the current is zero, $K=0$, and its velocity is given by

$$fV=-\frac{1}{\rho}\frac{\partial p}{\partial n}=f_oV_g$$

as follows from (8). V_g is the geostrophic velocity and f_o the value of the Coriolis parameter at the latitude of the Countercurrent. At point M the trajectory may have a radius of curvature $R=120$ km., as can be seen from figure 6A. It will be assumed that the normal pressure gradient remains constant along the trajectory, $-\frac{1}{\rho}\frac{\partial p}{\partial n}=f_oV_g$. With this assumption equation (8) becomes

$$KV^2+fV=f_oV_g$$

With $1/K=120$ km., $f=2.15\times10^{-5}$ sec.$^{-1}$ at latitude 8.5°, $f_o=1.65\times10^{-5}$ sec.$^{-1}$ at latitude 6.5°, and a geostrophic velocity $V_g=55$ cm./sec., it follows that $V=37$ cm./sec. at point M. This shows that the velocity decreases along the trajectory from 55 cm./sec. at point N to 37 cm./sec. at point M. The length of the trajectory between points N and M is approximately 450 km., thus the value of $\frac{\partial V}{\partial s}$ in equation (7) can be calculated. It follows that $\frac{1}{\rho}\frac{\partial p}{\partial s}=1.8\times10^{-5}$ cm. sec.$^{-2}$. Expressed in terms of dynamic topography, this means that the particle arrived at point M at a value 0.83 dynamic cm. higher than when it left point N, compared with a total difference of about 14 dynamic cm. across the current. The trajectory crosses the isobars at a very small angle, which is given by $tg\alpha=\frac{\partial p}{\partial s}\Big/\frac{\partial p}{\partial n}$. With $\frac{1}{\rho}\frac{\partial p}{\partial n}=90.7\times10^{-5}$ cm. sec.$^{-2}$ it follows that $\alpha=1.1°$.

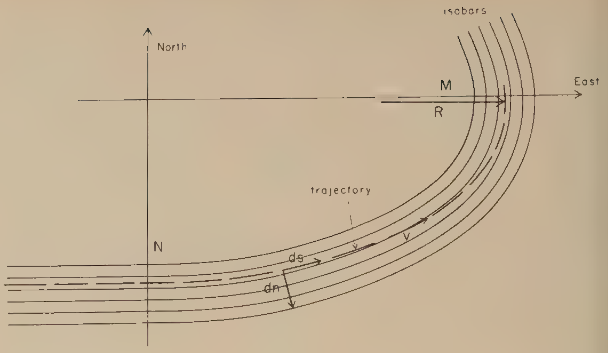

FIGURE 10.—Diagram showing schematically the isobars of a current flowing east and turning north. (The broken line is a trajectory, cutting the isobars under a small angle, R is the radius of curvature.)

Because the trajectories cut the isobars, the velocity V along the trajectory can be split into one component v parallel to the isobars and another component u normal to the isobars. The angle between the two sets of curves is so small that v will be almost as big as V, while u can be calculated from the relation $u/v=\frac{\partial p}{\partial s}\Big/\frac{\partial p}{\partial n}$, giving $u=0.92$ cm./sec. Over a distance of 450 km. and a depth of 20 m. this velocity normal to the isobars causes a transport of 8.3×10^{10} cm.^{3}/sec. across the isobars from the left side of the current to its right side. This calculation of the cross isobar transport compares very well with the figure of 7×10^{10} cm.^{3}/sec. calculated for the amount of upwelling from the thermal balance of the dome. Consequently, I conclude that the upwelling in the Costa Rica Dome is an effect of the northward turning of parts of the Countercurrent. The cross isobar circulation associated with such a turning current causes the upwelling, which is situated along the left flank of this cyclonic flow. This upwelling is, however, especially effective in the Costa Rica Dome, because the thermocline along the left flank of the Countercurrent is already in a shallow position before the current starts turning. As a consequence of this, an intense enrichment of the thin surface layer with nutrients is possible in the Costa Rica Dome.

In order to conserve the mass transport of the current, the product *V D*, where *D* is the depth of the current, must remain constant along a trajectory. This increase in the depth of the current in the direction of its flow is well documented in figure 7, where its depths increase progressively as the current proceeds from section *A* to sections *B* and *C*. The difference of dynamic height across the current remains unchanged during its progress, while the surface velocity decreases and the depth of the current increases. Thus the transport across the isobars can be interpreted as upwelling on the left flank of the current and sinking on its right flank.

PERMANENCE OF THE COSTA RICA DOME

The above discussions of the structure of the dome and its circulation have been based chiefly on one survey, but it is worthwhile to investigate whether or not the Costa Rica Dome is a permanent feature of the circulation and how far it is subject to seasonal variations. So far eight expeditions (table 1) have crossed or touched the area of the Costa Rica Dome, and all of them have found the dome in approximately the same position. As the dome is characterized by an extremely high position of the thermocline, the depth of the 19° C. isotherm, which coincides approximately with the center of the thermocline, is charted for six of the expeditions in figure 11. On the eighth crossing of the dome in February 1960 only BT observations were taken (fig. 1). During all these expeditions the 19° C. isotherm was found to be in less than 20 m. depth in the dome area. Along the periphery of the dome it was always below 40 m. Because some of the expeditions did only touch the dome or may not have crossed through its center, the size of the dome cannot be determined. The position of the dome during the different expeditions is given in table 1 and it can be seen that the dome maintains its position within 2° of latitude and longitude. It is situated between lat. 8° and 10° N. and between long. 88° and 90° W. Although the position of the dome was approximately the same during all these surveys, the circulation around the dome seems to have been considerably different, as indicated by the topographies of the 19° C. isotherm.

TABLE 1.—*Positions of the Costa Rica Dome on different expeditions*

Expedition	Date	Position of the dome		Reference for data
		Latitude °N.	Longitude °W	
Shuttle	May 1952	9.5	90	Unpublished.[1]
Shellback	July–Aug. 1952.	9	88	Unpublished.[1]
Eastropic	Oct.–Nov. 1955.	9	89.5	Scripps Institution of Oceanography, 1956.
Scope	Nov.–Dec. 1956.	8.5	89	Holmes and others, 1958.
Scot	May 1958	10	89	Holmes and Blackburn, 1960.
TO–59–1	Feb. 1959	9	89	Blackburn and others, 1962.
Costa Rica Dome.	Nov.–Dec. 1959.	8	88	Scripps Institution of Oceanography, 1960.
Explorer	Feb. 1960	9	89	Stewart, 1962.

Six of these expeditions, made between 1952 and 1959, cover the months between May and December; during this period the Countercurrent is always present. During February and especially in March, the Countercurrent is absent in this area and the cyclonic circulation is only weakly developed, as indicated in the surface charts by Cromwell and Bennett (1959). Thus, it might be possible that the dome would not be developed during this period. In February 1959 the area of the dome was crossed on expedition TO–59–1, and in February 1960 it was crossed by the vessel *Explorer*. On both crossings the dome was found to be in about the same position as during the other expeditions, and the 19° C. isotherm was well above 20 m. depth, as can be seen from the BT section taken by the *Explorer* (fig. 1). It is, however, not known whether or not the Countercurrent was developed during these times, or whether the Costa Rica Dome is persistent enough to remain for an appreciable time during the period in which the Countercurrent is not indicated in the surface current observations.

From the comparison of the results of these eight expeditions it can be concluded that the

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[1] Data available at Scripps Institution of Oceanography, and will be included in Oceanic observations of the Pacific, 1952, to be published by the University of California Press.

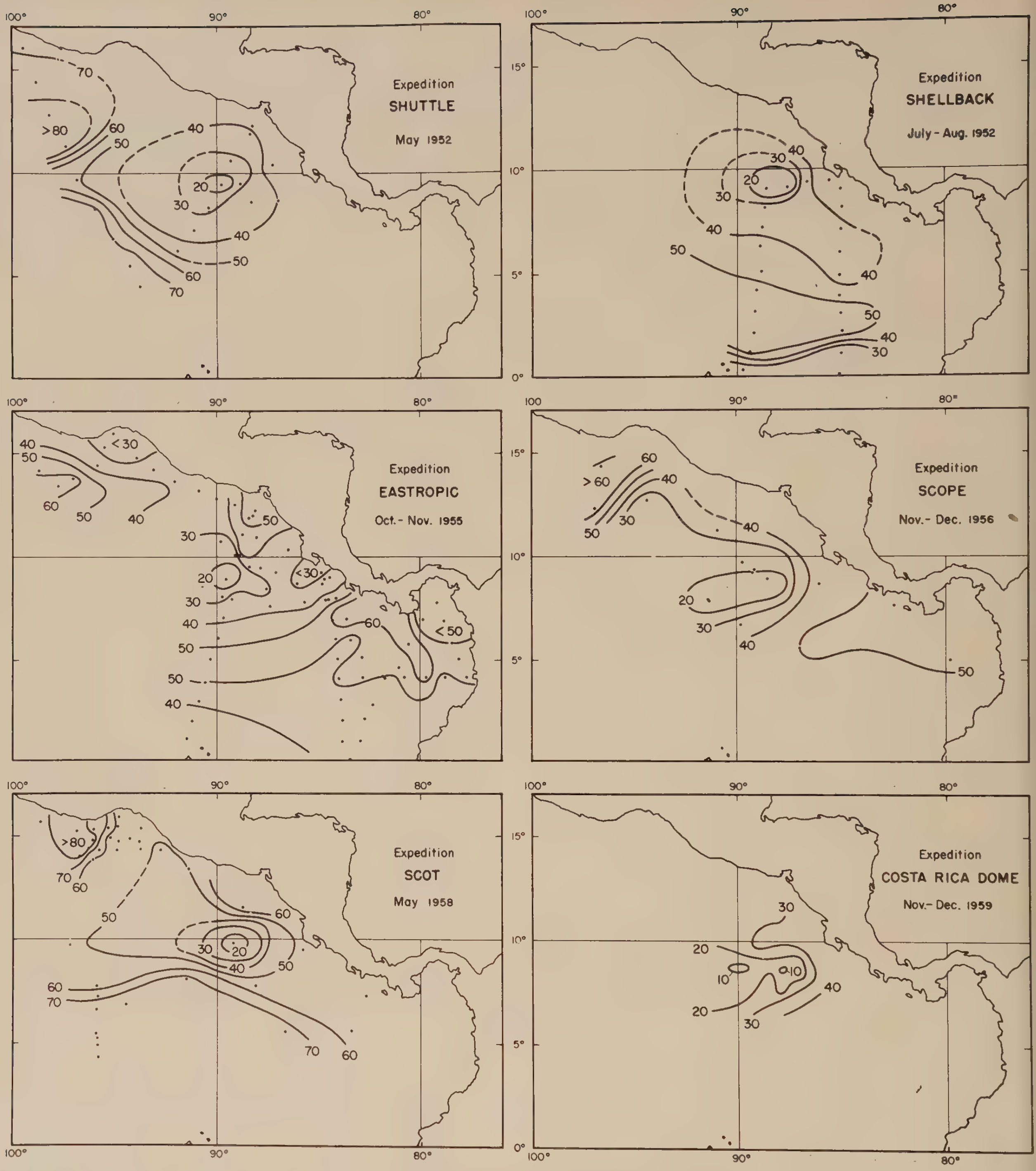
100°
90°
80°
15°
10°
5°
0°
Expedition SHUTTLE May 1952
70
>80
60
50
40
20
30
40
50
60
70
Expedition SHELLBACK July-Aug. 1952
30
40
20
30
40
50
40
50
40
30
40
50
<30
60
50
40
Expedition EASTROPIC Oct.-Nov. 1955
30
50
20
<30
30
40
60
<50
50
50
40
60
>60
40
30
50
Expedition SCOPE Nov.-Dec. 1956
40
20
30
40
50
>80
70
60
50
Expedition SCOT May 1958
60
30
20
40
50
60
70
70
60
Expedition COSTA RICA DOME Nov.-Dec. 1959
30
20
10
10
40
20
30

FIGURE 11.—Topography of the 19° C. isotherm in meters during six expeditions in the area of the Costa Rica Dome and its vicinity.

Costa Rica Dome is a permanent feature of the thermocline topography in the eastern tropical Pacific Ocean and that it varies very little in its position. A comprehensive survey of the Costa Rica Dome in February and March would be desirable to confirm the existence of the dome during these months and to determine the character of the associated circulation.

CONCLUSIONS

The analysis of the hydrographic structure of the Costa Rica Dome and of its circulation, based on the Costa Rica Dome cruise and the comparison with seven less complete surveys, eads to the following conclusions:

1. The Costa Rica Dome is a more or less circular area where the thermocline is extremely high and extremely sharp and where the top of the thermocline reaches to within a few meters of the sea surface. This area, about 200 km. in diameter, is characterized by slightly lower surface temperatures, higher salinity and phosphate contents, and reduced percentage of oxygen saturation. The average position of the dome is lat. 9° N., long. 89° W., and the fluctuations of the center of the dome are within ±1° of latitude and longitude, as a comparison of eight surveys demonstrates. Thus, the Costa Rica Dome is a permanent feature of the circulation in the eastern tropical Pacific Ocean.

2. The circulation around the dome is determined by the Equatorial Countercurrent in the south, the Costa Rica Coastal Current in the east, and parts of the North Equatorial Current in the north. Off the coast of Costa Rica these currents form a cyclonic circulation in the center of which the dome is situated. The Costa Rica Dome is the very pronounced eastern end of a ridge in the topography of the thermocline extending along the northern boundary of the Countercurrent. From the cyclonic circulation around the dome large eddies seem to separate and to contribute to large-scale mixing. One of them was observed during the Costa Rica Dome survey transporting 20 million m.^{3}/sec.

3. The northward turning of the Countercurrent requires an adjustment of its velocity distribution and causes a cross-circulation which produces upwelling in the dome. The upwelling in the dome must be in thermal balance which limits the average ascending velocity to 10^{-4} cm./sec. The total contribution of the upwelling s only 7×10^{10} cm.^{3}/sec., and the ascending water comes from layers immediately beneath the trong thermocline out of 75–200 m. depth where he temperature is 12°–14° C.

4. The upwelling in the Costa Rica Dome is a hallow process restricted to the surface layer and the thermocline. The amount of upwelling is very small because the intensity is less and the area much smaller than, for instance, that off the coast of Peru (Wyrtki, 1963). However, the effect of this upwelling on the enrichment of the surface layer in the Costa Rica Dome is considerable because of the much higher initial position of the thermocline and of the abundance of nutrient rich water immediately beneath the thin surface layer.

LITERATURE CITED

Blackburn, Maurice, Raymond C. Griffiths, Robert W. Holmes, and William H. Thomas.
1962. Physical, chemical, and biological observations in the eastern tropical Pacific Ocean: three cruises to the Gulf of Tehuantepec, 1958–59. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 420, 170 pp.

Brandhorst, Wilhelm.
1958. Thermocline topography, zooplankton standing crop, and mechanisms of fertilization in the eastern tropical Pacific. Conseil Permanent International pour l'Exploration de la Mer, Journal du Conseil, vol. 24, No. 1, pp. 16–31.

Budyko, M. I.
1956. The heat balance of the earth's surface. Leningrad, 255 pp. Translated by U.S. Department of Commerce, Weather Bureau, 1958.

Cromwell, Townsend.
1958. Thermocline topography, horizontal currents and "ridging" in the eastern tropical Pacific. Inter-American Tropical Tuna Commission Bulletin, vol. 3, No. 3, pp. 135–164.

Cromwell, Townsend, and Edward B. Bennett.
1959. Surface drift charts for the eastern tropical Pacific Ocean. Inter-American Tropical Tuna Commission Bulletin, vol. 3, No. 5, pp. 217–237.

Fuglister, Frederick C., and L. V. Worthington.
1951. Some results of a multiple ship survey of the Gulf Stream. Tellus, vol. 3, No. 1, pp. 1–14.

Holmes, Robert W., and others.
1958. Physical, chemical, and biological oceanographic observations obtained on Expedition Scope in the eastern tropical Pacific, November-December 1956. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 279, 117 pp.

Holmes, Robert W., and Maurice Blackburn.
1960. Physical, chemical, and biological observations in the eastern tropical Pacific Ocean: Scot Expedition, April–June 1958. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 345, 106 pp.

Knauss, John A.
1961. The structure of the Pacific Equatorial Countercurrent. Journal of Geophysical Research, vol. 66, No. 1, pp. 143–155.

Montgomery, Raymond B.

1939. Ein Versuch, den vertikalen und seitlichen Austausch in der Tiefe der Sprungschicht im äquatorialen Atlantischen Ozean zu bestimmen. Annalen der Hydrographie und Maritimen Meteorologie, Band 67, pp. 242–246.

Reid, Joseph L., Jr.

1962. On circulation, phosphate-phosphorus content. and zooplankton volumes in the upper part of the Pacific Ocean. Limnology and Oceanography, vol. 7, No. 3, pp. 287–306.

Scripps Institution of Oceanography.

1956. Data collected by Scripps Institution vessels on Eastropic Expedition. SIO Reference Report 56–28, 156 pp. (mimeo.)

Scripps Institution of Oceanography.

1960. Physical, chemical and biological data Costa Rica Dome cruise. SIO Reference Report 60–20 33 pp. (mimeo.)

Stewart, Harris B., Jr.

1962. Oceanographic cruise report, USC & GS Ship Explorer—1960. U.S. Department of Commerce, Coast and Geodetic Survey, Washington, D.C. 162 pp.

Wyrtki, Klaus.

1963. The horizontal and vertical field of motion in the Peru Current. Bulletin of the Scripps Institution of Oceanography, vol. 8, No. 4, pp. 313–346.

PRECONSTRUCTION STUDY OF THE FISHERIES OF THE ESTUARINE AREAS TRAVERSED BY THE MISSISSIPPI RIVER-GULF OUTLET PROJECT[1, 2]

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Bureau of Commercial Fisheries

ABSTRACT

Hydrographical and biological data were collected from April 1959 through March 1961 at selected stations in the marsh and bayou areas traversed by the Mississippi River-Gulf Outlet Channel between New Orleans and Breton Sound to provide preconstruction data needed for later assessment of the effects on the fauna of such a wide and deep channel connected at the Gulf end with water of high salinity. The channel will raise salinities over most of the project area. This should not greatly affect the fishes of the area which are preponderately euryhaline. It should have an adverse effect on abundance of the blue crab. The possible effect on the white shrimp is obscured by their avoidance of the open waters of Lake Borgne and their preference for the shoal protected marshes.

The Mississippi River-Gulf Outlet Project of the Corps of Engineers is a deep-water navigation hannel from New Orleans to the Gulf of Mexico (fig.1). The route traverses the marshes along the southwestern shore of Lake Borgne and then uts across the intricate system of bayous to Breton Sound. The deep channel crosses Breton Sound just to the north of Breton Island. The ompleted channel will be 36 feet deep and 500 eet wide at the bottom. The channel was redged in three stages: first, an access channel 18 feet deep by 140 feet wide, second, an interim hannel 36 feet deep by 250 feet wide; and third, he full-scale channel.

The channel traverses a marsh and estuarine rea of great value for waterfowl, muskrats, yster culture, sport and commercial fishing, and, erhaps the most important, for a nursery area tilized by the young of fish and shrimp that are ater harvested in great quantities in deeper ater outside of the project area.

The principal aim of this study was to determine the environmental and biological conditions prevailing prior to channel construction from the fishery standpoint. A preconstruction study on such a large scale was lacking, and it was hoped that comparison with a later postconstruction study of the same area would be invaluable, both in deciding on what effects, if any, could be attributed to the present project, and in forming a basis on which to predict the effect of similar projects in the future.

Note.—Approved for publication April 9, 1963.

[1] The data on which this report is based were collected by the Texas A. and M. Research Foundation for the Bureau of Sport Fisheries and Wildlife of the U.S. Fish and Wildlife Service under Contracts No. 14-16-008-523; No. 14-16-008-572; and No. 14-17-008-119. The Foundation released three mimeographed reports referred to as Reference 59-5T, Reference 59-21T, and Reference 61-20F. The original data are archived at the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex. All species identifications are by the Research Foundation. The author assumes sole responsibility for this analysis and the conclusions reached.

[2] Contribution No. 167 Bureau of Commerical Fisheries Biological Laboratory, Galveston, Tex.

[3] Present address: Alabama Marine Resources Laboratory, Dauphin Island, Alabama.

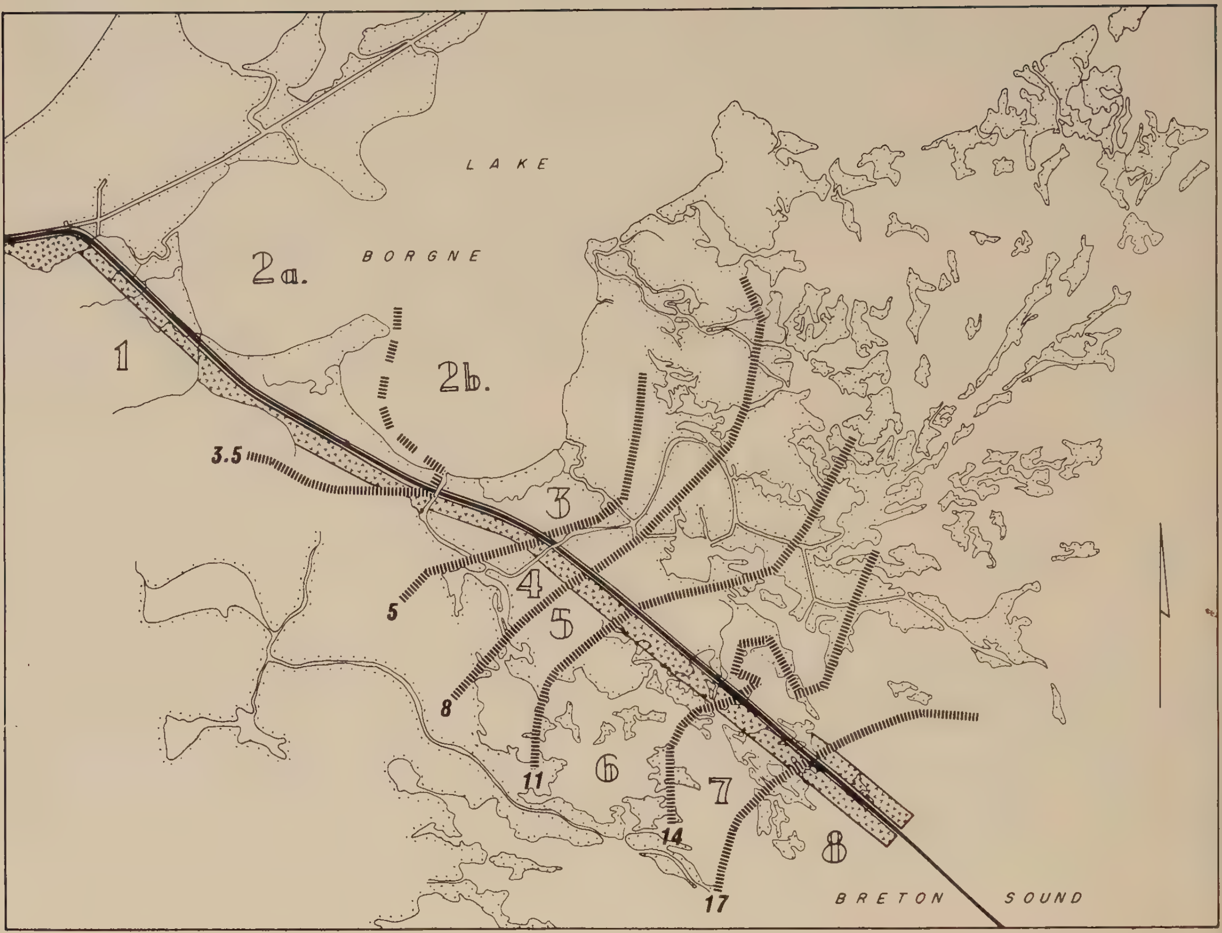


FIGURE 1.—The project areas showing the alignment of the Gulf Outlet channel as far as Breton Sound. (The shaded area along the southwest border of the channel is the 4,000-foot strip used as a spoil area. The shaded lines crossing the channel are isohalines that effectively divide the project area into smaller areas. The isohalines are based on average 24-month salinities.)

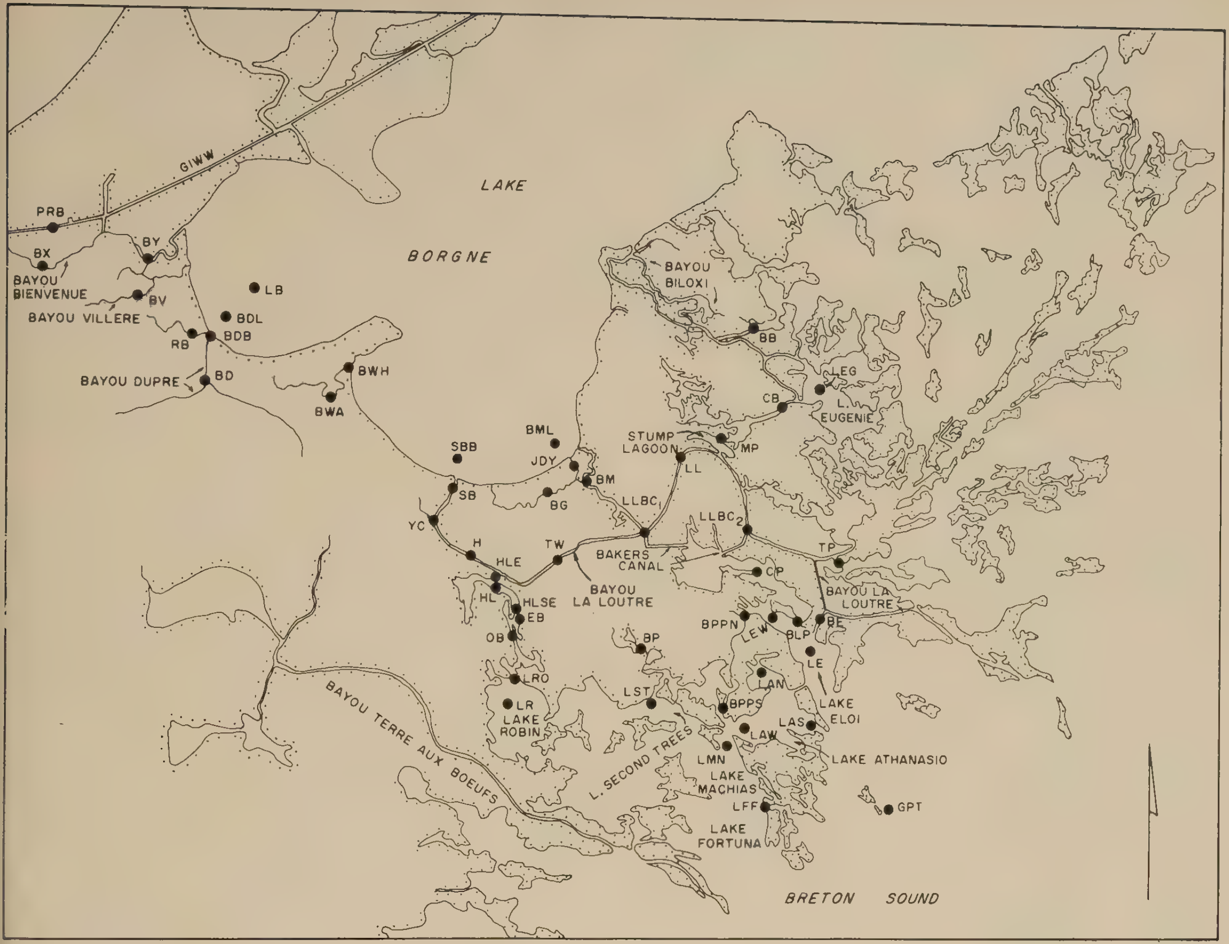
Dredging of the small access channel was commenced at the Gulf Intracoastal Waterway in May of 1959 and completed to Breton Sound by March of 1961. Some segments of the channel were dredged to the "interim" cross section during this period. Where they crossed the channel, certain bayous were kept open: Bayou Bienvenue, Bayou Villere, Bayou Dupre, Bayou Yscloskey, and Bayou La Loutre.

Following recommendations of the Fish and Wildlife Service, the Corps erected spoil retention dikes around a 4,000-foot strip along the southwestern boundary of the channel so that the solids could settle out from the liquid mud poured out from the hydraulic dredges. This measure effectively kept down sedimentation in the adjacent bayous.

HYDROGRAPHIC METHODS

Commencing in April 1959, stations were occupied at various points throughout the project area. At this time the exact route of the southern portion of the channel had not been decided but a route slightly northeast of the one finally chosen was then being favorably considered. Consequently, several stations occupied for a few weeks early in the study period were later abandoned, and a few more southerly stations added. The station locations are shown in figure 2. Table 1 lists the stations and the months each was occupied for hydrographical and biological observations.

Hydrographic observations were taken at each visit to a station (about once each 10 days through August 1960 and twice a month thereafter), and


GIWW
LAKE
BORGNE
PRB
BX
BY
BAYOU
BIENVENUE
BV
LB
BAYOU VILLERE
BDL
RB
BDB
BAYOU DUPRE
BD
BWH
BWA
BAYOU
BILOXI
BB
LEG
CB
L.
EUGENIE
STUMP
LAGOON
MP
LL
BML
SBB
JDY
BM
SB
BG
LLBC1
LLBC2
YC
H
HLE
TW
BAKERS
CANAL
BAYOU
LA LOUTRE
TP
CP
BAYOU LA
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ROBIN
LST
LAN
BPPS
LAKE
ELOI
LAS
LAW
BAYOU TERRE AUX BOEUFS
L. SECOND TREES
LMN
LAKE
MACHIAS
LAKE ATHANASIO
LFF
GPT
LAKE
FORTUNA
BRETON SOUND

IGURE 2.—The project area showing all of the sampling stations mentioned in this report. (For details see table 1.)

bout three times daily (except on weekends) at he base station at Hopedale. They included alinity, temperature, dissolved oxygen, phoshates, turbidity, and alkalinity.

alinity

At the base station at Hopedale, about 43 perent of the salinities were determined by titration, he remainder by use of a portable battery-operted conductivity meter. A continuously recordng conductivity meter was also used at Hopedale, ut checks against titrations show the records to e too unreliable for use.

ater temperature

Water temperature was measured in centigrade rom bucket samples of surface water. The emperatures were similar at any one time throughout the project area, and therefore, are without value in characterizing the bodies of water.

Dissolved oxygen

Dissolved oxygen in milliliters per liter was determined by a modified Winkler method. Oxygen values fluctuated so erratically from day to day at the base station that their usefulness is very questionable. Only in a very few instances in which heavy sewage contamination was suspected, were the oxygen values sufficiently low to be detrimental to the fauna.

The modified Winkler method used employed 100 g. of KOH and 50 g. of KI per 1,000 ml. of distilled water. This has been found to be an unreliable method for most estuarine waters because of the high organic content. Marvin,

TABLE 1.—*List of stations by area and months sampled*

Area	Station		Months sampled					
			Hydrography			Biology		
	Symbol	Name	1959	1960	1961	1959	1960	1961
1	BX	Bayou Bienvenue at Paris Road.	7	12	3	----	----	----
	PRB	Intracoastal Waterway at Paris Road Bridge.	7	8	----	----	----	----
	BV	Bayou Villere	3	12	3	----	----	----
	BY	Bayou Bienvenue at Y	7	12	3	----	----	----
	BD	Bayou Dupre	7	12	3	4	12	3
	RB	Rotten Bayou	2	12	3	4	12	3
	BDB	Bayou Dupre Beacon	7	12	3	4	10	3
	BWH	Bayou Lewis	7	12	3	----	----	----
	BWA	Bayou Grand	7	8	----	----	----	----
2a	BDL	Bayou Dupre Light	7	12	3	4	12	3
	LB	Lake Borgne (off Bayou Dupre).	----	12	3	----	12	3
2b	SBB	Shell Beach Beacon	9	12	3	----	----	----
	BML	Bayou St. Malo Light	8	12	3	4	12	3
3	SB	Shell Beach	9	12	3	----	8	3
	YC	Bayou Yscloskey	9	12	3	----	----	----
	H	Hopedale	9	12	3	----	----	----
	BM	Bayou St. Malo	9	12	3	4	12	3
	BG	Bayou Guyago	8	12	3	4	12	3
	JDY	Jahnckes Ditch at Y	2	12	3	4	12	3
4	BB	Bayou Biloxi	6	----	----	----	----	----
	MP	Mike's Pass	5	----	----	----	----	----
	LL	Bayou La Loutre	6	----	----	----	----	----
	LLBC 1	La Loutre-Bakers Canal, west.	9	12	3	----	----	----
	TW	Bayou La Loutre Survey Tower.	9	12	3	----	----	----
	HLE	Hopedale Lagoon entrance.	1	----	----	----	----	----
	HL	Hopedale Lagoon	9	12	3	----	----	----
	HLSE	Hopedale Lagoon, southeast.	2	----	----	----	----	----
	EB	East Bayou	2	----	----	----	----	----
	OB	Oyster Bay	9	12	3	----	----	----
5	LEG	Lake Eugenie	6	----	----	----	----	----
	CB	Crooked Bayou	6	----	----	----	----	----
	LLBC 2	La Loutre-Bakers Canal, east.	9	8	----	----	----	----
	CP	China Pass	----	5	3	----	----	----
	LRO	Lake Robin-Oyster Bay	2	3	----	----	2	----
	LR	Lake Robin	9	12	3	----	----	----
6	TP	Treasure Pass	9	8	----	----	----	----
	BE	Bayou Eloi	----	----	----	1	----	----
	LE	Lake Eloi	9	12	3	----	----	----
	LEW	Lake Eloi, west	----	----	----	1	----	----
	BPPN	Bayou Pointe en Pointe, north.	9	12	3	4	12	3
	BPPS	Bayou Pointe en Pointe, south.	9	6	----	----	----	----
	LST	Lake of Second Trees	9	12	3	----	----	----
	BP	Bayou Pisana	9	11	3	----	----	----
	BLP	Blind Pass	----	----	----	1	----	----
7	LAS	Lake Athanasio, south	3	12	3	3	11	3
	LAN	Lake Athanasio, north	3	8	----	3	7	----
	LAW	Lake Athanasio, west	2	----	----	2	----	----
	LMN	Lake Machias, north	2	12	3	2	11	3
8	LFF	Lake Fortuna, at Bayou Frenepiquant.	2	12	3	1	11	3
	GPT	Grace Point	----	3	3	----	3	3

Zein-Eldin, May, and Lansford (1960) use 900 g. of NaI and 400 g. of NaOH in only 550 ml. of distilled water to overcome the errors produced from high turbidities.

Inorganic phosphate

Inorganic phosphate was determined by a colorimetric method. The values show great and erratic variations, which could be caused by particulate phosphate in the unfiltered samples. This explanation is corroborated by an apparent correlation between turbidity and phosphates.

Turbidity

Turbidity was measured with a Klett colorimeter. The readings were converted into grams per liter of oven-dried suspended solids by comparison with a predetermined curve. The samples were shaken vigorously before making readings so that the values include heavy particles which might not be transported any distance by the water, but be present in the samples wholly because of local wave action.

Average turbidities were slightly lower in general in areas of higher salinity. The dredging operations occasionally caused much higher than average turbidities. Thus, the turbidity at Shell Beach (SB) and Yscloskey (YC) was extremely high (twice the average) during February and March 1961. The interim channel dredging from Bayou Dupre to Bayou Yscloskey reached Bayou Yscloskey in February 1961 and might easily account for extreme turbidities in these closely adjacent stations.

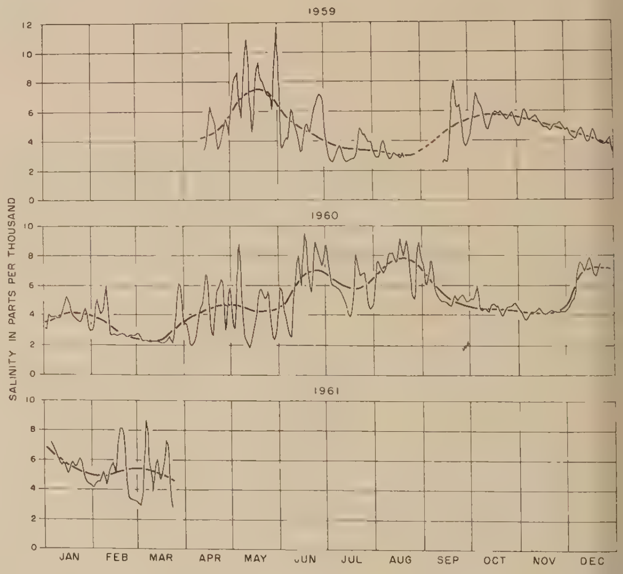

FIGURE 3.—Daily salinities at the base station (H) in Hopedale. (See text for details.)

SALINITY

The hydrographical changes that the Gulf outlet channel might be expected to cause would be chiefly changes in salinities and currents. For this reason, we have paid particular attention to these two features. The daily salinities at the base station at Hopedale (see H, fig. 2) are given in table 2. These were smoothed by first interpolating for the missing weekend days and then smoothing by 3–s with double weight on the center item (fig. 3). The trend line has been drawn by eye.

TABLE 2.—*Mean daily salinity at Hopedale, La.*

[Parts per thousand]

Day	Month																							
	1959									1960												1961		
	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
	-----	5.64	9.95	3.87	-----	-----	4.36	-----	4.85	-----	3.01	2.67	4.21	-----	6.66	-----	4.87	8.09	-----	4.14	4.42	-----	4.14	2.98
	-----	6.53	3.45	4.30	-----	-----	4.16	4.76	5.03	-----	3.06	3.14	-----	2.62	5.89	-----	9.41	5.14	-----	4.35	4.34	-----	4.48	3.01
	-----	8.63	3.18	2.85	2.76	-----	-----	5.33	4.17	-----	3.97	2.25	-----	2.94	4.36	-----	6.61	-----	5.00	3.87	-----	7.21	4.67	2.82
	-----	8.33	3.81	-----	2.91	-----	-----	6.20	4.34	4.27	6.20	2.25	1.79	3.75	-----	-----	7.96	-----	5.23	3.45	-----	7.12	-----	-----
	-----	8.62	4.24	-----	3.22	-----	7.69	6.38	-----	3.70	4.02	-----	1.95	10.20	-----	5.61	6.68	7.84	6.90	-----	5.29	7.21	-----	-----
	-----	8.73	-----	2.44	4.05	-----	7.06	5.50	-----	3.92	-----	-----	1.98	9.17	3.37	6.28	-----	.7.81	5.14	-----	4.59	6.83	4.46	9.28
	-----	5.90	-----	2.90	4.16	-----	6.20	-----	4.07	3.96	-----	2.32	2.32	-----	2.38	5.66	-----	7.06	4.11	4.11	6.78	-----	5.65	9.04
	-----	4.54	4.00	3.06	-----	-----	6.73	-----	4.09	.3 89	4.23	2.25	2.62	-----	2.33	5.95	7.03	5.29	-----	4.31	7.08	-----	5.22	5.22
	-----	-----	7.35	3.45	-----	-----	6.13	5.25	4.70	-----	5.11	2.28	-----	1.66	3.30	-----	7.97	5.46	-----	4.24	7.89	6.26	3.46	3.94
0	-----	-----	6.08	3.93	2.72	-----	-----	5.83	4.83	-----	8.20	2.17	-----	2.76	5.14	-----	8.51	-----	4.59	4.14	-----	5.60	4.98	3.33
1	-----	11.49	4.55	-----	2.78	-----	-----	5.32	4.94	3.74	2.87	2.18	5.00	1.65	-----	5.51	7.75	-----	4.31	4.21	-----	5.60	-----	-----
2	-----	10.90	5.34	-----	2.77	-----	4.72	5.97	-----	4.06	2.60	-----	4.14	1.76	-----	5.60	8.41	4.79	4.06	-----	6.72	5.91	-----	-----
3	3.01	7.42	-----	2.62	3.13	2.34	4.47	5.38	-----	4.87	-----	-----	5.58	1.75	8.76	4.81	-----	5.05	4.36	-----	7.21	5.83	5.91	6.91
4	3.06	6.10	-----	2.68	3.20	2.36	5.28	-----	3.79	4.79	-----	2.26	7.13	-----	7.05	4.91	-----	4.91	4.85	4.67	7.48	-----	5.68	4.67
5	3.68	3.36	2.08	2.52	-----	2.96	5.37	-----	3.92	5.54	2.70	2.22	7.12	-----	3.77	3.60	7.05	-----	-----	4.02	8.43	-----	4.78	4.32
6	3.88	-----	3.32	2.65	-----	2.58	5.94	5.04	3.72	-----	2.76	2.20	-----	3.49	8.90	-----	8.82	-----	-----	4.03	7.44	4.68	5.48	5.14
7	5.30	-----	3.75	2.74	2.91	2.47	-----	4.79	4.59	-----	2.51	2.12	-----	4.77	10.20	-----	9.65	-----	4.53	4.11	-----	6.17	8.13	5.44
8	6.62	8.77	5.86	-----	2.67	2.57	-----	4.77	5.17	4.29	2.71	2.09	2.32	4.96	-----	4.40	8.21	-----	4.53	4.00	-----	5.78	-----	-----
9	-----	10.80	4.88	-----	3.19	-----	5.91	5.13	4.47	3.87	2.75	-----	2.29	6.21	-----	7.51	7.62	4.51	4.56	-----	6.43	5.86	-----	-----
0	5.07	6.84	-----	2.79	3.91	-----	5.76	4.51	-----	4.03	-----	-----	3.68	5.67	6.06	9.09	-----	5.37	3.80	-----	6.78	5.33	8.13	8.24
1	5.82	8.92	-----	3.06	4.26	9.10	6.08	-----	3.91	3.70	-----	2.32	6.28	-----	5.06	6.75	-----	5.57	3.88	4.45	7.35	-----	7.84	4.32
2	3.40	7.78	4.42	3.80	-----	6.94	5.94	-----	3.88	3.63	2.70	3.05	5.56	-----	5.63	6.52	9.74	4.85	-----	4.22	7.44	-----	4.96	3.28
3	3.38	-----	6.36	5.62	-----	6.07	5.51	5.00	3.70	-----	2.43	2.02	-----	4.83	8.88	-----	6.44	4.88	-----	4.18	7.85	6.23	3.53	2.52
4	3.42	-----	6.29	4.29	-----	6.07	-----	5.19	3.76	-----	2.58	1.93	-----	5.97	9.17	-----	5.36	-----	4.63	4.31	-----	6.18	3.32	2.67
5	-----	6.93	6.42	-----	-----	6.80	-----	4.96	3.57	3.53	2.66	2.44	6.92	5.68	-----	6.93	5.57	-----	4.50	4.14	-----	5.19	-----	-----
6	-----	7.15	7.14	-----	-----	-----	5.32	-----	-----	4.17	2.61	-----	4.46	3.91	-----	6.89	4.22	5.51	4.70	-----	-----	5.00	-----	-----
7	-----	7.17	-----	4.44	-----	-----	5.73	5.32	-----	4.85	-----	-----	2.56	2.09	7.44	4.60	-----	5.05	4.37	-----	-----	4.48	3.32	-----
8	5.97	6.56	-----	3.51	-----	3.51	6.08	-----	3.93	4.34	-----	6.57	2.21	-----	7.22	4.44	-----	4.79	4.97	4.28	-----	-----	3.04	-----
9	4.82	3.94	7.21	3.95	-----	3.38	5.71	-----	4.59	2.99	2.65	6.33	7.38	-----	7.00	4.36	10.23	4.76	-----	4.20	-----	-----	-----	-----
0	3.62	14.41	6.14	4.18	-----	4.07	5.30	4.72	3.78	-----	-----	4.53	-----	2.80	9.47	-----	7.24	5.02	-----	4.23	-----	4.38	-----	-----
1	-----	11.25	-----	3.30	-----	-----	-----	-- -	2.82	-----	-----	2.12	-----	4.16	-----	-----	7.39	-----	4.45	-----	-----	4.13	-----	-----
ays	14	25	22	23	15	14	22	20	24	20	21	23	21	21	22	19	23	20	21	22	17	21	20	18
Average salinity	4.36	7.87	5.30	3.43	3.24	4.37	5.70	5.27	4.19	4.11	3.44	2.77	4.17	4.41	6.27	5.76	7.51	5.59	4.64	4.17	6.68	5.76	5.06	4.84
umber of observations	54	92	84	98	45	42	65	60	62	57	61	69	61	63	60	50	56	39	42	44	33	41	38	35
itrated observations [1]	54	92	84	90	1	33	1	4	6	8	61	54	61	24	9	2	15	0	1	0	0	0	0	0

[1] All nontitrated observations made with a portable conductivity meter.

Two facts are clearly shown by figure 3: the day-by-day variations in salinity are extreme, and ver the 2-year period there is no consistent seasonal pattern.

The first step in determining the cause of salinity variations was to obtain as nearly as possible a icture of the average salinities in different sections of the project area over the entire 24-month period. The average monthly salinity at each station is given in table 3. In some cases, it has been possible to nterpolate missing data on a proportional basis from adjacent stations with similar characteristics. hese interpolated values are shown in parentheses.

TABLE 3.—*Mean monthly salinity at each station*

[Parts per thousand]

Date	Station[1]																	
	BX		PRB		BD		BV		BY		RB		BDB		BDL		LB	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
1959																		
April	------	(1.50)	------	(1.91)	------	(2.21)	------	(2.26)	------	(2.32)	------	(2.53)	------	(2.58)	------	(2.74)	------	(2.82)
May	5	1.15	2	1.58	8	1.79	------	(1.48)	8	1.52	------	(1.70)	8	1.73	5	2.13	------	(2.20)
June	4	0.91	4	1.55	4	1.55	------	(1.42)	4	1.45	------	(1.68)	4	1.71	4	1.83	------	(1.89)
July	5	1.15	5	1.38	5	1.49	------	(1.44)	5	1.48	------	(1.55)	5	1.58	5	1.80	------	(1.86)
August	1	0.82	1	1.10	1	1.53	------	(1.46)	1	1.50	------	(1.50)	1	1.53	1	1.68	------	(1.73)
September	------	(1.00)	------	(1.27)	------	(1.47)	------	(1.51)	------	(1.55)	------	(1.69)	------	(1.72)	------	(1.83)	------	(1.89)
October	3	2.82	3	2.64	3	2.82	3	3.87	3	4.00	------	(4.73)	4	4.82	4	5.13	------	(5.29)
November	3	2.27	3	3.19	3	3.04	3	3.42	3	3.52	1	3.24	3	3.23	3	3.38	------	(3.48)
December	3	2.41	3	2.32	4	3.01	3	2.95	3	2.99	4	3.01	4	3.13	4	2.97	------	(3.06)
1960																		
January	3	1.37	3	1.87	2	2.36	3	2.47	3	2.03	2	2.60	2	2.53	2	2.74	1	2.26
February	3	1.02	3	1.32	3	1.62	3	1.85	3	1.46	3	1.62	3	1.70	6	1.99	3	1.79
March	3	0.80	3	1.37	3	1.58	3	1.86	3	1.48	3	1.52	3	1.59	3	1.58	3	1.58
April	3	0.95	3	1.06	3	1.09	3	1.23	3	1.46	3	1.28	3	1.54	3	1.36	3	1.21
May	3	1.11	3	1.25	3	1.29	3	1.18	3	1.29	3	1.27	3	1.32	3	1.31	3	1.25
June	3	1.27	3	1.36	3	1.67	3	1.53	3	1.51	3	1.53	3	1.62	3	1.37	3	1.69
July	3	2.23	3	2.45	3	3.09	3	1.62	3	2.71	3	3.36	3	3.23	3	3.63	3	4.08
August	3	1.63	2	3.38	3	3.39	3	3.31	3	3.45	3	3.80	3	3.88	3	4.23	3	4.83
September	2	2.82	------	(3.58)	2	4.79	2	4.18	2	4.38	2	4.49	2	5.26	2	5.34	2	5.72
October	2	1.56	------	(1.98)	2	3.13	2	3.04	2	3.40	2	3.54	2	3.53	2	3.98	2	4.16
November	2	1.98	------	(2.51)	2	3.35	2	3.35	2	3.26	2	3.40	2	3.54	2	3.64	2	3.35
December	2	4.16	------	(5.28)	2	5.97	2	5.59	2	5.48	2	6.20	2	6.30	2	6.48	2	6.37
1961																		
January	2	1.66	------	(2.11)	2	1.88	2	3.34	2	4.22	2	4.40	2	4.11	2	4.76	2	5.07
February	2	1.14	------	(1.45)	2	1.81	2	2.48	2	2.35	2	3.12	2	2.75	2	3.10	2	3.36
March	2	1.24	------	(1.57)	2	1.32	2	1.92	2	1.42	2	1.76	2	1.80	2	1.84	2	2.12

[Parts per thousand]

Date	Station[1]																	
	BWA		BWH		SBB		SB		JDY		BML		BG		YC		BM	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
1959																		
April	------	(3.00)	------	(3.02)	3	3.49	10	3.77	------	(4.04)	------	(3.81)	------	(4.26)	11	3.78	2	4.42
May	2	2.26	2	2.24	2	3.71	3	7.15	------	(5.43)	1	6.07	3	4.62	3	7.59	4	5.93
June	4	2.23	4	2.22	4	2.79	4	3.88	------	(3.39)	4	3.31	4	3.50	4	3.98	4	3.70
July	5	2.00	5	1.96	5	2.83	5	2.70	------	(3.34)	5	3.13	5	3.30	5	2.73	5	3.65
August	1	2.08	1	1.92	1	2.97	1	3.02	------	(2.53)	1	2.66	1	3.21	1	2.82	1	2.77
September	------	(2.01)	------	(2.02)	1	2.33	1	2.25	------	(2.21)	1	2.31	1	2.54	1	2.29	1	2.41
October	3	4.98	3	5.26	3	6.21	3	6.42	------	(5.72)	3	6.50	3	5.96	3	5.91	3	6.25
November	3	4.67	3	4.72	3	5.14	3	5.10	1	4.85	3	5.19	3	5.48	3	4.68	2	5.24
December	3	3.66	3	3.57	3	4.07	3	4.29	3	4.14	3	3.93	3	4.17	3	3.99	3	4.07
1960																		
January	3	3.21	3	3.58	3	3.60	3	3.99	2	3.66	2	3.73	2	3.84	3	4.01	2	3.58
February	3	2.79	3	2.59	3	2.68	3	2.68	3	2.99	3	2.89	5	2.29	3	2.80	3	3.18
March	3	2.03	3	2.20	3	2.20	3	2.24	3	2.50	3	2.32	3	2.50	3	2.14	3	2.49
April	3	1.78	3	1.52	5	1.74	3	1.79	3	1.91	3	1.63	3	2.67	3	3.76	3	2.16
May	3	1.61	3	1.56	6	2.09	3	2.28	3	2.29	3	2.18	3	3.14	3	3.42	3	3.42
June	4	2.08	4	2.00	7	2.78	4	2.59	3	3.69	3	3.69	3	4.24	4	6.08	3	6.23
July	2	3.15	2	3.07	5	4.02	2	3.62	3	5.40	3	5.43	3	6.07	2	6.50	3	5.49
August	2	3.30	3	3.72	3	4.50	3	4.68	3	4.89	3	5.13	3	5.25	3	7.61	3	5.57
September	------	(4.95)	2	4.98	3	5.21	3	5.11	3	5.41	3	5.37	3	5.61	3	5.30	3	5.45
October	------	(4.27)	2	4.30	4	4.28	2	4.47	2	4.24	2	4.20	2	4.40	2	4.32	2	4.36
November	------	(3.75)	2	3.78	4	3.83	2	3.59	2	3.93	2	4.07	2	4.01	2	3.95	2	3.99
December	------	(7.73)	2	7.78	4	6.15	2	6.26	2	5.84	2	6.48	2	5.84	2	6.16	2	6.40
1961																		
January	------	(4.71)	2	4.74	4	6.42	2	6.29	2	6.60	2	6.80	2	6.54	2	5.83	2	6.70
February	------	(3.40)	2	3.42	4	4.24	2	5.28	2	4.74	2	4.52	2	5.04	2	3.02	2	4.90
March	------	(2.09)	2	2.10	4	3.12	2	3.15	2	4.48	2	3.38	2	4.98	2	3.99	2	5.02

See footnotes at end of table.

TABLE 3.—*Mean monthly salinity at each station*—Continued

Date	Station [1]																	
	HLE		HL		TW		HLSE		LLBC$_1$		EB		LL		BB		OB	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
1959																		
pril	4	5.38	12	6.24	4	5.93	7	6.31	5	7.27	4	6.62	5	7.33	1	7.88	4	7.58
ay	------	------	4	10.77	5	10.67	1	8.71	6	14.98	1	9.06	5	13.96	2	12.52	4	12.38
une	------	------	4	8.90	4	3.70	------	------	8	9.79	------	------	4	11.09	4	9.06	4	10.44
uly	------	------	5	4.95	6	5.26	------	------	10	6.27	------	------	7	6.37	5	7.24	5	6.63
ugust	------	------	1	4.87	1	4.28	------	------	1	7.49	------	------	1	6.67	1	6.70	1	5.97
eptember	------	------	1	4.59	3	5.44	------	------	3	4.64	------	------	1	8.73	1	9.03	1	5.41
ctober	------	------	2	5.26	2	6.16	------	------	4	5.66	------	------	------	------	------	------	2	5.74
ovember	------	------	3	5.69	2	5.40	------	------	5	6.13	------	------	------	------	------	------	3	6.34
ecember	------	------	3	4.80	3	6.66	------	------	3	5.73	------	------	------	------	------	------	3	6.32
1960																		
anuary	------	------	3	5.02	3	4.93	------	------	3	5.49	------	------	------	------	------	------	3	5.87
ebruary	------	------	3	3.92	3	3.78	------	------	2	3.13	------	------	------	------	------	------	3	5.24
arch	------	------	3	2.66	5	4.73	------	------	3	3.30	------	------	------	------	------	------	3	4.26
pril	------	------	3	6.28	2	4.76	------	------	3	6.47	------	------	------	------	------	------	3	6.44
ay	------	------	3	3.94	3	5.71	------	------	3	6.61	------	------	------	------	------	------	3	6.80
une	------	------	3	9.21	3	10.85	------	------	3	11.91	------	------	------	------	------	------	3	11.57
uly	------	------	3	9.55	3	10.60	------	------	3	11.96	------	------	------	------	------	------	3	11.08
ugust	------	------	3	9.72	3	7.50	------	------	3	8.40	------	------	------	------	------	------	3	12.57
eptember	------	------	3	7.10	2	5.51	------	------	3	6.86	------	------	------	------	------	------	3	9.52
ctober	------	------	2	5.54	2	4.68	------	------	2	5.60	------	------	------	------	------	------	2	7.04
ovember	------	------	2	4.07	2	4.18	------	------	2	4.74	------	------	------	------	------	------	2	4.36
ecember	------	------	2	6.81	2	7.86	------	------	2	7.84	------	------	------	------	------	------	2	8.14
1961																		
anuary	------	------	2	6.37	2	8.91	------	------	2	6.44	------	------	------	------	------	------	2	6.60
ebruary	------	------	2	6.64	2	5.59	------	------	2	6.49	------	------	------	------	------	------	2	7.79
arch	------	------	2	5.95	2	6.27	------	------	2	6.68	------	------	------	------	------	------	2	7.80

Date	Station																	
	MP		LRO		CB		LR		LEG		CP		LLBC$_2$		BP		BPPN	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
1959																		
pril	------	(8.50)	5	8.13	1	8.72	4	9.43	1	8.57	------	------	4	10.68	2	12.80	2	12.96
ay	3	14.00	2	14.02	2	14.36	2	11.89	2	15.63	------	------	4	18.49	3	16.20	2	19.58
une	4	11.74	------	------	4	11.86	6	6.38	4	12.61	------	------	4	14.08	4	14.12	4	16.49
uly	5	7.82	------	------	5	8.82	5	7.70	5	9.34	------	------	5	11.61	5	9.75	5	11.22
ugust	1	8.35	------	------	1	9.09	1	7.45	1	8.35	------	------	1	11.18	1	9.39	1	12.37
ptember	1	10.00	------	------	1	10.12	1	8.45	1	10.00	------	------	1	6.02	1	8.77	1	8.38
ctober	------	------	------	------	------	------	2	7.68	------	------	------	------	2	8.40	2	9.75	2	10.92
ovember	------	------	------	------	------	------	3	8.19	------	------	------	------	4	8.25	3	11.98	3	9.64
ecember	------	------	------	------	------	------	3	7.60	------	------	------	------	3	8.90	2	11.99	3	9.47
1960																		
nuary	------	------	------	------	------	------	3	6.36	------	------	------	------	3	8.52	3	9.50	1	10.92
bruary	------	------	------	------	------	------	3	8.41	------	------	------	------	3	6.01	2	11.57	4	7.63
arch	------	------	------	------	------	------	3	7.40	------	------	------	------	3	5.66	3	9.79	3	6.29
pril	------	------	------	------	------	------	3	8.42	------	------	------	------	3	9.39	3	9.76	3	10.56
ay	------	------	------	------	------	------	3	6.49	------	------	------	------	3	8.25	3	9.77	3	9.45
ne	------	------	------	------	------	------	3	12.34	------	------	------	------	3	16.80	3	15.47	3	17.83
ly	------	------	------	------	------	------	3	13.57	------	------	------	------	3	14.29	3	14.72	3	17.12
ugust	------	------	1	10.57	------	------	3	14.29	------	------	1	12.60	2	11.70	3	13.42	3	13.78
ptember	------	------	3	9.20	------	------	3	10.20	------	------	3	7.32	------	(7.40)	3	9.86	3	9.21
tober	------	------	1	8.90	------	------	2	8.06	------	------	2	7.32	------	(6.83)	1	7.91	2	11.13
ovember	------	------	------	------	------	------	2	5.88	------	------	2	6.06	------	(5.34)	2	7.94	2	6.96
ecember	------	------	------	------	------	------	2	9.10	------	------	2	9.46	------	(10.74)	------	(16.50)	2	11.60
1961																		
nuary	------	------	------	------	------	------	2	8.40	------	------	2	10.19	------	(10.32)	1	12.60	2	11.76
bruary	------	------	------	------	------	------	2	8.40	------	------	2	9.52	------	(9.81)	1	9.97	2	11.78
arch	------	------	------	------	------	------	2	9.49	------	------	2	8.59	------	(9.93)	2	11.64	2	11.69

[1] See footnotes at end of table.

Table 3.—*Mean monthly salinity at each station*—Continued

Date	Station[1]																			
	TP		LST		LE		BPPS		LAW		LAN		LMN		LAS		LFF		GPT	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
1959																				
April	5	13.19	2	12.97	2	15.20	2	14.06	-----	--------	-----	(15.12)	-----	(16.39)	-----	(17.12)	-----	(18.85)	-----	--------
May	4	20.88	3	17.23	4	22.39	3	20.39	-----	--------	-----	(21.27)	-----	(23.06)	-----	(24.09)	-----	(26.53)	-----	--------
June	4	18.99	4	15.78	4	17.50	4	18.00	-----	--------	-----	(17.86)	-----	(19.37)	-----	(20.23)	-----	(22.28)	-----	--------
July	5	13.64	5	11.38	5	13.56	5	13.51	-----	--------	-----	(13.39)	-----	(14.52)	-----	(15.16)	-----	(16.70)	-----	--------
August	1	14.35	1	10.87	1	15.40	1	13.86	-----	--------	-----	(14.11)	-----	(15.29)	-----	(15.98)	-----	(17.59)	-----	--------
September	1	10.40	1	10.40	1	14.30	1	13.00	-----	--------	-----	(13.26)	-----	(14.38)	-----	(15.02)	-----	(16.54)	-----	--------
October	2	12.52	2	11.55	2	14.80	2	13.49	2	14.44	2	13.50	-----	(15.34)	2	16.91	-----	(17.65)	-----	--------
November	3	10.12	3	12.83	3	12.05	3	12.30	1	13.00	3	12.76	2	12.36	3	13.14	-----	(16.66)	-----	--------
December	3	10.19	3	10.10	3	12.22	1	13.64	-----	--------	2	11.70	2	13.64	3	13.68	1	14.58	-----	--------
1960																				
January	3	10.55	3	8.49	3	11.07	2	11.13	-----	--------	2	14.16	2	12.03	1	13.93	2	14.88	-----	--------
February	3	8.12	3	11.36	3	8.47	3	12.16	-----	--------	3	11.97	3	12.43	3	12.41	3	13.39	-----	--------
March	3	5.57	3	9.88	3	9.53	3	9.63	-----	--------	3	10.15	3	10.41	3	11.10	3	12.74	-----	--------
April	3	12.13	3	11.26	3	12.73	3	11.97	-----	--------	3	11.90	3	12.53	3	14.77	3	15.18	-----	--------
May	3	9.75	3	9.53	3	10.43	3	9.63	-----	--------	3	12.73	3	12.26	3	14.39	3	12.30	-----	--------
June	3	17.12	3	16.59	3	18.85	3	18.14	-----	--------	3	19.16	3	20.48	3	21.83	3	20.79	-----	--------
July	3	15.89	3	15.86	3	16.80	-----	(18.03)	-----	--------	3	18.40	3	18.58	3	21.33	3	22.53	-----	--------
August	2	15.42	3	15.20	3	15.30	-----	(17.28)	-----	--------	2	13.84	3	15.41	3	16.73	3	17.61	-----	--------
September	-----	(9.09)	3	11.70	3	9.99	-----	(13.30)	-----	--------	-----	(11.47)	3	12.00	3	12.99	3	14.07	-----	--------
October	-----	(8.39)	2	8.05	2	9.22	-----	(9.15)	-----	--------	-----	(8.69)	2	9.76	2	9.84	2	10.64	2	9.98
November	-----	(6.56)	2	9.08	2	7.21	-----	(10.32)	-----	--------	-----	(8.62)	2	10.32	2	9.76	2	10.76	2	11.05
December	-----	(13.20)	2	17.59	2	14.50	-----	(20.00)	-----	--------	-----	(14.02)	1	17.80	2	15.88	2	22.33	2	20.36
1961																				
January	-----	(12.68)	2	13.55	2	13.93	-----	(15.41)	-----	--------	-----	(17.25)	2	16.23	2	19.54	2	20.78	2	19.76
February	-----	(12.05)	2	8.72	2	13.24	-----	(9.91)	-----	--------	-----	(11.69)	2	11.18	2	13.24	2	12.34	2	15.98
March	-----	(12.19)	2	13.32	2	13.40	-----	(15.14)	-----	--------	-----	(13.49)	2	18.24	2	15.28	2	19.40	2	20.84

[1] Means in parentheses interpolated by comparison of observed data with adjacent stations.
See table 1 for interpretation of symbols.

The data of tables 2 and 3 are summarized in table 4 by bimonthly periods. Observations are too scant, considering the degree of variation in respect to the mean, to be able to place reliance on means derived from any shorter period of time. A 24-month mean salinity is also shown for every station. Admittedly, the 24-month means may be somewhat unreliable when interpolated for stations with but a few months' data, but they are the best estimates available, and their consistency has given us considerable confidence in their use.

From the 24-month mean salinities of table 4, the isohalines of figure 1 are plotted. These have formed the basis for dividing the project area into the numbered areas shown, which will be referred to again under the discussion of the biology.

CURRENTS

The question now is what causes the observed 24-month salinity pattern and the short-term fluctuations therein. An attempt to utilize the data from hourly current observations taken for periods from 12 to 24 hours' duration was unsuccessful, chiefly because of the extremely limited number of stations occupied. (All but 4 out of 42 observation periods were taken at stations H and YC.)

Thereafter, resort was had to the 568 observations on the direction of flow at 10 different stations made at the times these stations were visited by field observers (table 5).

From these field observations, figure 4 has been plotted to show the percent of time the current flowed in various directions at each station at which currents were observed. Figure 4 has been made semidiagrammatic to show the main routes water can follow as it moves across the project area. There appears to be a residual current flowing north in Bayou La Loutre from $LLBC_2$ that continues around the loop in the bayou past station LL. At $LLBC_1$ a portion of this water together with some from Lake Borgne turns south, but a portion continues west where it meets a residual eastward-flowing current from station YC. These observations are of great interest for they indicate the presence of a residual southerly current from Lake Borgne, entering the bayou system at both Bayou Yscloskey (SB) and Bayou St. Malo (BM).

TABLE 4.—*Summary of mean salinities for all stations*

[Parts per thousand]

Station	1959					1960						1961				
	24-month average	Apr.-May	June-July	Aug.-Sept.	Oct.-Nov.	Dec.-Jan.	Feb.-Mar.	Apr.-May	June-July	Aug.-Sept.	Oct.-Nov.	Dec.-Jan.	Feb.-Mar.	Mean of two bimonthly periods		
														High	Low	Difference
X	1.62	1.32	1.03	0.91	2.54	1.89	0.91	1.03	1.75	2.22	1.77	2.91	1.19	2.72	0.91	1.81
RB	2.06	1.74	1.46	1.18	2.91	2.10	1.34	1.16	1.90	3.48	(2.24)	(3.70)	(1.51)	3.59	1.17	2.42
D	2.39	2.00	1.52	1.50	2.93	2.68	1.60	1.19	2.38	4.09	3.24	3.92	1.56	4.00	1.34	2.66
V	2.45	(1.87)	(1.43)	(1.48)	3.64	2.71	1.86	1.20	1.58	3.74	3.19	4.46	2.20	4.10	1.32	2.78
Y	2.51	1.92	1.46	1.52	3.76	2.51	1.47	1.38	2.11	3.92	3.33	4.85	1.88	4.38	1.42	2.96
B	2.73	(2.12)	(1.62)	(1.60)	3.98	2.80	1.57	1.28	2.44	4.14	3.47	5.30	2.44	4.72	1.42	3.30
DB	2.78	2.16	1.64	1.62	4.02	2.83	1.64	1.43	2.42	4.57	3.54	5.20	2.28	4.88	1.52	3.36
DL	2.95	2.44	1.82	1.76	4.26	2.86	1.78	1.34	2.50	4.78	3.81	5.62	2.47	5.20	1.55	3.65
B	3.04	(2.51)	(1.88)	(1.81)	(4.38)	2.66	1.68	1.23	2.88	5.28	3.76	5.72	2.74	5.50	1.46	4.04
WA	3.24	2.63	2.12	2.04	4.82	3.44	2.41	1.70	2.62	4.12	(4.01)	(6.22)	(2.74)	5.52	1.87	3.65
WH	3.26	2.63	2.09	1.97	4.99	3.58	2.40	1.54	2.54	4.35	4.04	6.26	2.76	5.62	1.76	3.86
BB	3.77	3.60	2.81	2.65	5.68	3.84	2.44	1.92	3.40	4.86	4.06	6.29	3.68	5.98	2.18	3.80
B	4.03	5.46	3.29	2.64	5.76	4.14	2.46	2.04	3.10	4.90	4.03	6.28	4.22	6.02	2.25	3.77
DY	4.09	(4.74)	(3.36)	(2.37)	5.28	3.90	2.74	2.10	4.54	5.15	4.08	6.22	4.61	5.75	2.24	3.51
ML	4.11	4.94	3.22	2.47	5.84	3.83	2.60	1.90	4.56	5.25	4.14	6.64	3.95	6.24	2.18	4.06
G	4.31	4.44	3.40	2.88	5.72	4.00	2.40	2.90	5.16	5.43	4.20	6.19	5.01	5.96	2.64	3.32
C	4.44	5.68	3.36	2.56	5.30	4.00	2.47	3.59	6.29	6.46	4.14	6.00	3.50	6.38	2.52	3.86
M	4.47	5.18	3.68	2.59	5.74	3.82	2.84	2.79	5.86	5.51	4.18	6.55	4.96	6.20	2.69	3.51
opedale	4.95	6.12	4.36	3.80	5.48	4.15	3.10	4.29	6.02	6.55	4.40	6.22	4.95	6.38	3.45	2.93
LE	5.34	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
L	6.20	8.50	6.92	4.73	5.48	4.91	3.29	5.11	9.38	8.41	4.80	6.59	6.30	8.94	4.01	4.93
W	6.22	8.30	4.48	4.86	5.78	5.80	4.26	5.24	10.72	6.50	4.43	8.38	5.93	9.55	4.34	5.21
LSE	6.81	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
LBC$_1$	7.08	11.12	8.03	6.06	5.90	5.61	3.22	6.54	11.94	7.63	5.17	7.14	6.58	11.53	4.42	7.11
B	7.11	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
L	7.17	10.64	8.73	7.70	------	------	------	------	------	------	------	------	------	------	------	------
B	7.24	10.20	8.15	7.86	------	------	------	------	------	------	------	------	------	------	------	------
B	7.58	9.98	8.54	5.69	6.04	6.10	4.75	6.62	11.32	11.04	5.70	7.37	7.80	11.18	5.22	5.96
P	7.92	11.25	9.78	9.18	------	------	------	------	------	------	------	------	------	------	------	------
RO	8.32	11.08	------	------	------	------	------	------	------	9.88	------	------	------	------	------	------
B	8.69	11.54	10.34	9.60	------	------	------	------	------	------	------	------	------	------	------	------
R	8.82	10.66	7.04	7.95	7.94	6.98	7.90	7.46	12.96	12.24	6.97	8.75	8.94	12.60	6.98	5.62
EG	8.90	12.10	10.98	9.18	------	------	------	------	------	------	------	------	------	------	------	------
P	9.85	------	------	------	------	------	------	------	------	9.96	6.69	9.82	9.06	------	------	------
LBC$_2$	9.94	14.58	12.84	8.60	8.32	8.71	5.84	8.82	15.54	9.55	(6.08)	(10.53)	(9.87)	15.06	5.96	9.10
P	11.47	14.50	11.94	9.08	10.86	10.74	10.68	9.76	15.10	11.64	7.92	14.55	10.80	14.82	8.50	6.32
PPN	11.61	16.27	13.86	10.38	10.28	10.20	6.96	10.00	17.48	11.50	9.04	11.68	11.74	16.88	8.00	8.88
P	12.21	17.04	16.32	12.38	11.32	10.37	6.84	10.94	16.50	12.26	(7.48)	(12.94)	(12.36)	16.77	7.16	9.61
ST	12.22	15.10	13.58	10.64	12.19	9.30	10.62	10.40	16.22	13.45	8.56	15.57	11.02	15.90	8.93	6.97
E	13.42	18.80	15.53	14.85	13.42	11.64	9.00	11.58	17.82	12.64	8.22	14.22	13.32	18.31	8.61	9.70
PPS	13.90	17.22	15.76	13.43	12.90	12.38	10.90	10.80	18.08	(15.29)	(9.74)	(17.70)	(12.52)	17.89	10.27	7.62
AW	14.63	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
AN	14.60	(13.20)	(15.62)	(13.68)	13.13	12.93	11.06	12.32	18.78	12.66	(8.66)	(15.64)	(12.59)	17.21	9.86	7.35
MN	14.75	(19.72)	(16.94)	(14.84)	13.85	12.84	11.42	12.40	19.53	13.70	10.04	17.02	14.71	19.62	10.73	8.89
AS	15.60	(20.60)	(17.70)	(15.50)	15.02	13.80	11.76	14.58	21.58	14.86	9.80	17.71	14.26	21.09	10.78	10.31
FF	16.96	(22.69)	(19.49)	(17.06)	(17.16)	14.73	13.06	13.74	21.66	15.84	10.70	21.56	15.87	22.18	11.88	10.30
PT	17.27	------	------	------	------	------	------	------	------	------	10.52	20.06	18.41	------	------	------

TABLE 5.—*Observations on current directions from regular sampling trips*

[Percent of observations]

Direction	Station										
	SB	YC	HL	OB	TW	BM	LLBC$_1$	LL	LLBC$_2$	TP	Average
o current	1.4	7.0	10.9	4.6	13.6	7.1	4.9	52.2	2.0	9.8	11.4
oward Lake Borgne	38.6	26.8	------	------	------	39.3	20.5	------	------	------	31.3
way from Lake Borgne	60.0	66.2	------	------	------	50.0	[1] 45.5	------	------	------	55.4
oward Bayou La Loutre (north)	------	------	39.1	52.3	------	------	------	------	------	------	------
way from Bayou La Loutre (south)	------	------	48.6	43.1	------	------	------	------	------	------	------
oward Bayou Guyago (west)	------	------	------	------	------	3.6	------	------	------	------	------
oward LLBC$_1$ (east)	------	------	1.6	------	------	------	------	------	------	------	------
oward Hopedale (west)	------	------	------	------	74.2	------	30.6	39.1	------	------	48.0
oward Stump Lagoon (east)	------	------	------	------	12.1	------	6.0	8.7	------	------	8.9
oward LL (north)	------	------	------	------	------	------	------	------	49.0	------	------
way from LL (south)	------	------	------	------	------	------	------	------	6.1	------	------
oward Halfmoon Lagoon	------	------	------	------	------	------	------	------	33.7	------	------
way from Halfmoon Lagoon	------	------	------	------	------	------	------	------	7.1	------	------
oward Treasure Pass	------	------	------	------	------	------	------	------	2.0	------	------
way from Treasure Pass	------	------	------	------	------	------	------	------	73.0	------	------
oward Bayou Petre (north)	------	------	------	------	------	------	------	------	------	67.4	------
way from Bayou Petre (south)	------	------	------	------	------	------	------	------	------	21.5	------
est on Bayou Petre	------	------	------	------	------	------	------	------	------	33.9	------
ast on Bayou Petre	------	------	------	------	------	------	------	------	------	55.6	------
Number of days observed	70	71	64	65	66	28	81	23	49	51	56.8

[1] Toward Halfmoon Lagoon.

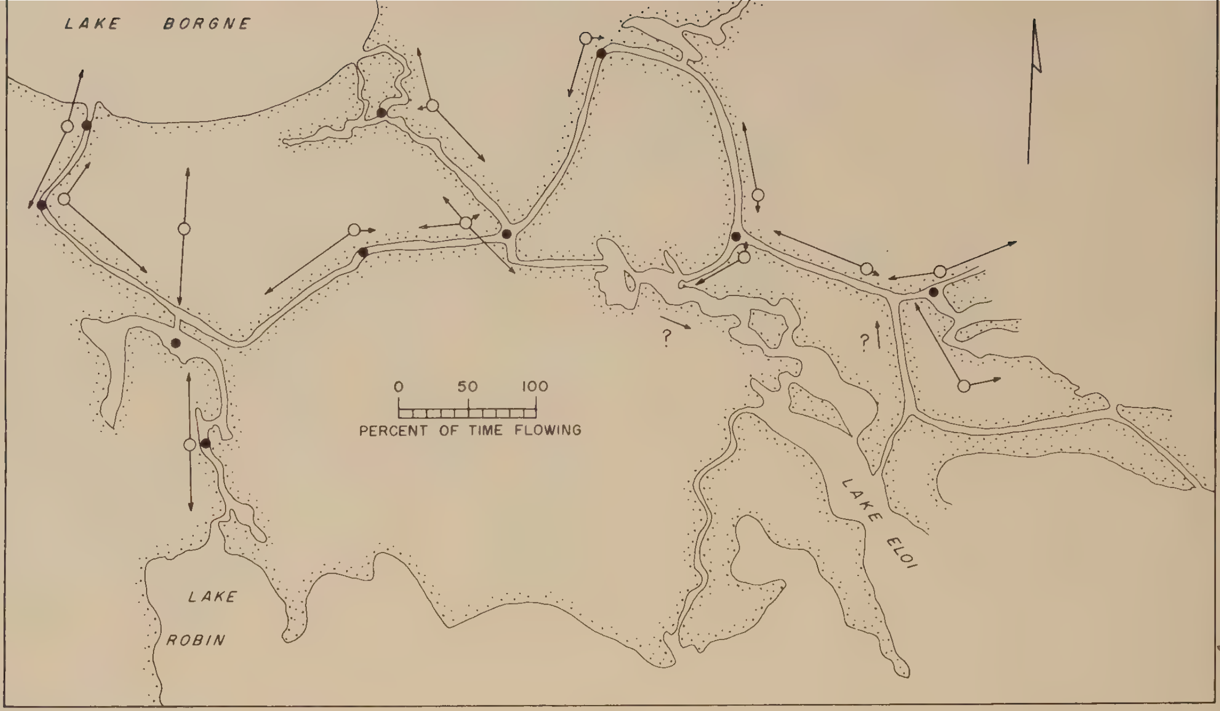

FIGURE 4.—Semidiagrammatic map of the project area showing the percent of time currents were flowing in each direction. Station locations shown by black dots. Length of arrows from adjacent open circles shows the percent of time in the indicated direction.

In addition to the two routes for water exchange between Lake Borgne and Breton Sound indicated in figure 4, there is a third route, via Bayou Biloxi, Lake Eugenie, Crooked Bayou, and Stump Lagoon (fig. 2), for which information is too scant to assess its actual significance. The effect of these main transport routes on mean salinities is shown in figure 5, in which 24-month salinities are plotted against distance from station SBB in Lake Borgne along the routes water would have to follow in order to circulate. The mean salinity along both the western and central routes between Breton Sound and where they meet the cross channels linking SB with LEG decreases at a rather uniform rate of 1°/oo every 2 miles.

On the crosslinking channels running from LEG to SB the rate of decrease in salinity is also quite uniform but only 1°/oo every 5 miles. This great contrast in the rate of decrease in salinity per mile between that of the two chief water routes from Breton Sound and that of the cross channel suggests that Lake Borgne dominates the water circulation north of Bayou La Loutre and

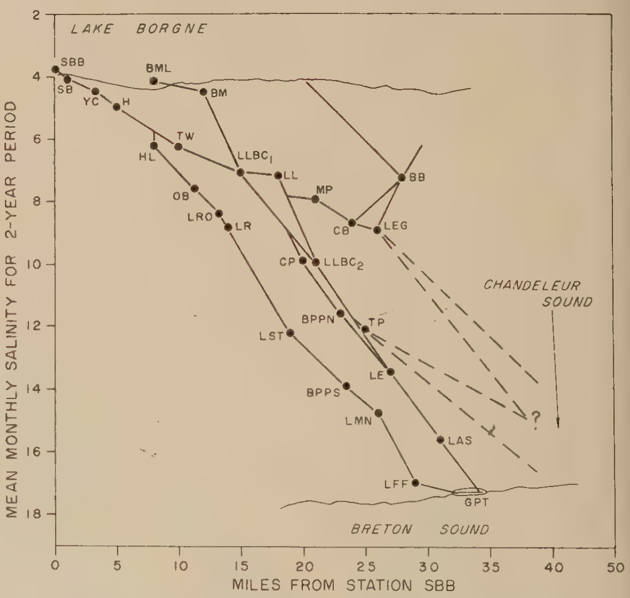

FIGURE 5.—Diagram to show the average relation between salinity and distance along the water exchange routes linking Lake Borgne with Breton and Chandeleur Sounds.

along Bayou La Loutre between Stump Lagoon and Lake Borgne.

The lack of data on the cross-sectional areas of the connecting waterways makes it difficult to estimate the relative importance of each route to the water exchange pattern. Some idea of their relative importance, however, can be gained by noting the relative variation in salinity, since the degree of variation should be positively correlated with the amount of water exchange.

Because of the paucity and nonorthogonal pattern of the sampling, I have been forced to utilize a very simple measure of variation; namely, the salinity difference between the average of the two highest bimonthly means and the average of the two lowest bimonthly means (table 4).

The logarithms of the resulting differences in salinity are plotted as the ordinate, labeled "salinity variation" in figure 6 using the mean monthly salinity for the entire 2-year period as the abscissa. Several features are of interest. The salinity variation in the central water transport system is considerably higher than in the western, indicating a greater water exchange. The great decrease in salinity variation between $LLBC_1$ and H on the linking stations tends to confirm this conclusion. It should also be noted that stations in Bayou Pisana (BP) and northern Lake Athanasio (LAN), which are in effect in cul-de-sacs without through movement of water, exhibit less variation than neighboring stations on the water transport route.

The four stations in Lake Borgne are similar in their degree of variation. The stations in area 3 (fig. 1) show approximately the same degree of variation as those of Lake Borgne. This tends to confirm my previous observation that a residual current flows southeastward from Lake Borgne since Lake Borgne obviously dominates these stations. In area 1, the stations exhibit a gradually lowering salinity coupled with decreased variation as they go from the lake shore toward Paris Road.

FACTORS AFFECTING SALINITY

Since the waters of Lake Borgne exert the major influence on salinities throughout the project area, I have attempted to determine to what extent certain measurable factors influence them. Table 6 gives data on the discharge of the Pearl River at Bogalusa, the intensity of the north and northeast wind components at the New Orleans Airport, and the average of the monthly salinities for four stations in Lake Borgne. As explained in the footnotes to the table, lagged averages have been used because both river discharge and wind take some time to effect major changes in salinity.

The isopleths for salinity of Lake Borgne plotted against these two variables are shown in figure 7. At low wind intensity from the north and northeast, there is a strong negative relationship between the discharge of the Pearl River and the resulting salinity in Lake Borgne. At higher wind intensities, the salinity rises considerably above the

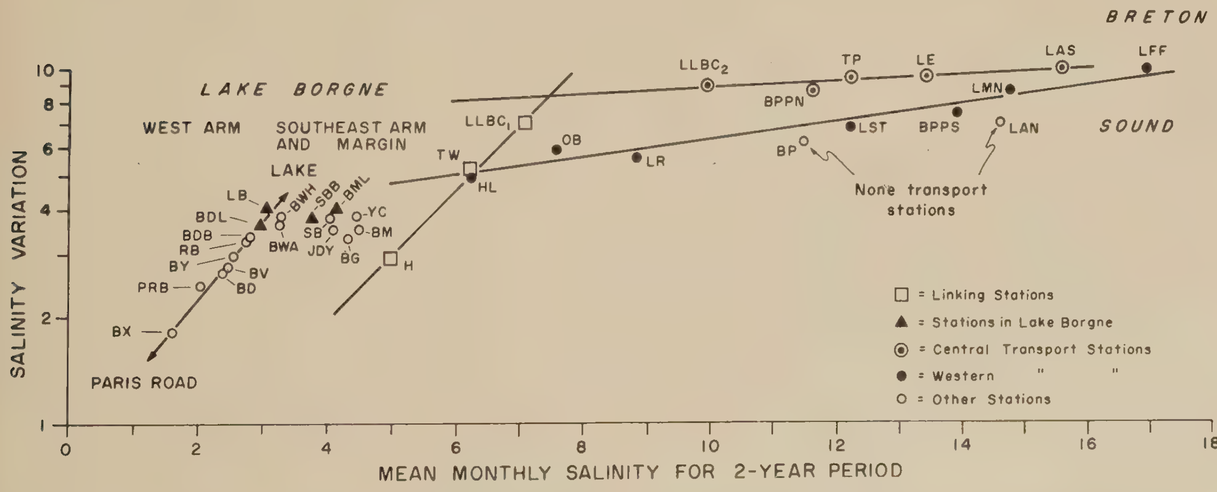

FIGURE 6.—Showing the variation in salinity in relation to mean salinity. The higher variation along the central transport route is indicative of a greater exchange of water through this system than through the western route.

TABLE 6.—*Factors influencing salinity of Lake Borgne*

Date	Fresh water		Wind		Salinity of Lake Borgne[2]
	Pearl River discharge		Wind intensity[1]		
	Month listed	Lagged average[3]	Month listed	Lagged average[4]	
1959	*Thousand c.f.s.*	*Thousand c.f.s.*			‰
February	18.86	----------	----------	----------	----------
March	10.51	----------	----------	----------	----------
April	10.86	12.32	71.7	(71.7)	3.28
May	7.93	9.62	22.9	39.2	3.54
June	9.05	8.96	31.1	28.3	2.54
July	4.29	6.92	17.2	21.8	2.43
August	3.01	4.73	41.3	33.3	2.28
September	2.66	3.13	69.2	59.9	[5] (2.18)
October	3.18	2.94	121.8	104.3	5.78
November	4.44	3.58	121.4	121.5	4.60
December	6.99	5.21	60.1	80.5	3.64
1960					
January	11.50	8.28	86.2	77.5	3.41
February	20.91	14.36	57.6	67.1	2.54
March	24.48	20.46	71.4	66.8	2.08
April	9.47	17.76	45.3	54.0	1.56
May	9.95	12.66	50.4	48.7	1.79
June	2.27	6.78	31.0	37.5	2.46
July	1.85	3.64	42.4	38.6	4.04
August	4.30	2.91	26.2	31.6	4.40
September	2.39	3.05	96.5	73.1	5.22
October	1.88	2.57	58.1	71.9	4.19
November	2.06	2.05	96.1	83.4	3.83
December	2.39	2.16	83.8	87.9	6.72
1961					
January	7.41	4.33	----------	----------	5.68
February	22.75	12.54	----------	----------	3.82
March	39.47	26.37	----------	----------	2.61

[1] Number of days times mean speed in knots.

[2] For stations BDL, BWH, SBB, and BML.

[3] Average for a period including month listed, previous month and half of second preceding month.

[4] Average for 6-week period, derived from average of month listed and half of preceding month's average times ⅔. Data are for New Orleans airport from U.S. Weather Bureau.

[5] Unreliable, only 2 salinity observations for Lake Borgne.

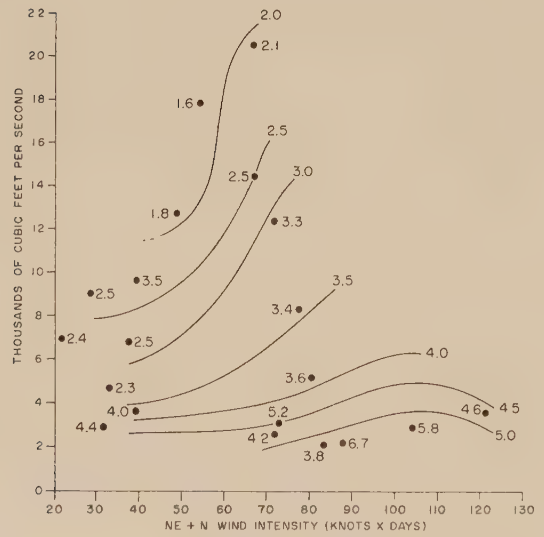

FIGURE 7.—Salinity isopleths in Lake Borgne under varying conditions of wind intensity and Pearl River discharge.

level dictated by river discharge. This is shown by the steep slope of the isopleths.

It would appear that the north and northeast direction of the wind causes intrusion into Lake Borgne of the more saline water of Mississippi Sound.

SUMMARY OF HYDROGRAPHY

In concluding the discussion of hydrography, several points can be noted:

1. Exchange between the low salinity waters of Lake Borgne and the higher salinity waters of Breton Sound takes place by three routes, the central route appears to carry more water than the western route.
2. Large, short-term fluctuations in salinity are especially pronounced in the bayous that form part of the water exchange route.
3. During the 24-month period of study, salinity trends at Hopedale were independent of season.
4. Salinity levels in Lake Borgne are controlled chiefly by fresh-water input (for which we used the discharge of the Pearl River) modified by wind direction and speed.
5. Pearl River discharge and wind intensity both require time to significantly affect salinities in the western end of Lake Borgne. This time lag appears to be several weeks for river discharge and about 2 weeks for wind intensity.
6. Salinity in areas 1 to 3 and the portion of area 4 from Bayou La Loutre northward is dominated by Lake Borgne salinity.

BIOLOGY

BIOLOGICAL SAMPLING

Biological sampling was carried out at selected stations since it was not considered feasible to collect at all stations. One of the major changes that could occur from the channel construction would be a change, probably a raising, in salinity levels. Therefore, it was decided to make collections in three areas that possessed relatively low, medium, and high salinity ranges. The mean bimonthly salinities for the stations actually sampled are given in table 7. It will be noted at once that hydrographical areas 4 and 5 shown in figure 1 were not sampled. Two-thirds of all of the otter trawl tows (the principal gear used) were made in areas 1 to 3 all of which are low salinity areas dominated by Lake Borgne.

TABLE 7.—*Mean bimonthly salinities in areas of biological sampling during periods actually sampled*

[Parts per thousand]

Date	Areas and stations						
	1	2a	2b	3	6	7	8
	BD, RB, BDB	BDL, LB	SBB, BML	BM, BG, JDY	BPPN[1]	LAS, LAN, LMN[2]	LFF[3]
1959							
June–July	1.59	1.85	3.02	3.48	13.86	--------	------
August–September	1.57	1.78	2.56	2.61	--------	--------	------
October–November	3.64	4.32	5.76	5.58	10.28	14.00	------
December–January	2.77	2.76	3.84	3.91	10.20	13.19	14.73
1960							
February–March	1.60	1.73	2.52	2.66	6.96	11.41	13.06
April–May	1.30	1.28	1.91	2.60	10.00	13.10	13.74
June–July	2.41	2.69	3.98	5.19	17.48	19.96	21.66
August–September	4.27	5.03	5.06	5.36	11.50	13.74	15.84
October–November	3.48	3.78	4.10	4.15	9.04	9.50	10.70
December–January	4.81	5.67	6.46	6.32	11.68	16.79	21.56
1961							
February–March	2.09	2.60	3.82	4.86	11.74	13.85	15.87
Monthly average	2.63	3.00	3.94	4.29	11.61	14.98	16.96

[1] Also samples from adjacent stations BE, LEW, and BLP during July, 1959.

[2] Also samples from LAW in October and November, 1959.

[3] Also samples from GPT from October 1960 to March 1961.

The number of otter trawl tows made in each area at different bimonthly salinities are shown in figure 8 and table 8. This concentration of biological sampling at one extreme of the salinity range has decreased the reliability of any prediction of the effects of moderate changes in salinity. Thus, table 7 shows no biological sampling in areas 4 and 5 leaving a gap between area 3 with an average salinity of 4.3‰ and area 6 with an average of 11.6‰.

TABLE 8.—*Sampling effort by otter trawl in each area*

[Number of 10-minute tows]

Date	Area						
	1	2a	2b	3	6	7	8
1959							
June–July	9	2.7	2	8	13.5	------	------
August–September	3	1	1	3	------	------	------
October–November	18	6	6	17.8	6	18.3	------
December–January	23	15.4	8	24.9	8	13	3
1960							
February–March	8.7	16	5	19	9	21	7
April–May	16.6	12	11	17.9	6	18	6
June–July	18	12	12	17.9	6	18	5
August–September	15	10	7	15	5	12	5
October–November	12	8	8	12	4	8	8
December–January	12	8	8	12	4	8	12
1961							
February–March	12	8	8	12	4	8	12
Total	147.3	99.1	76.0	159.5	65.5	124.3	58.0

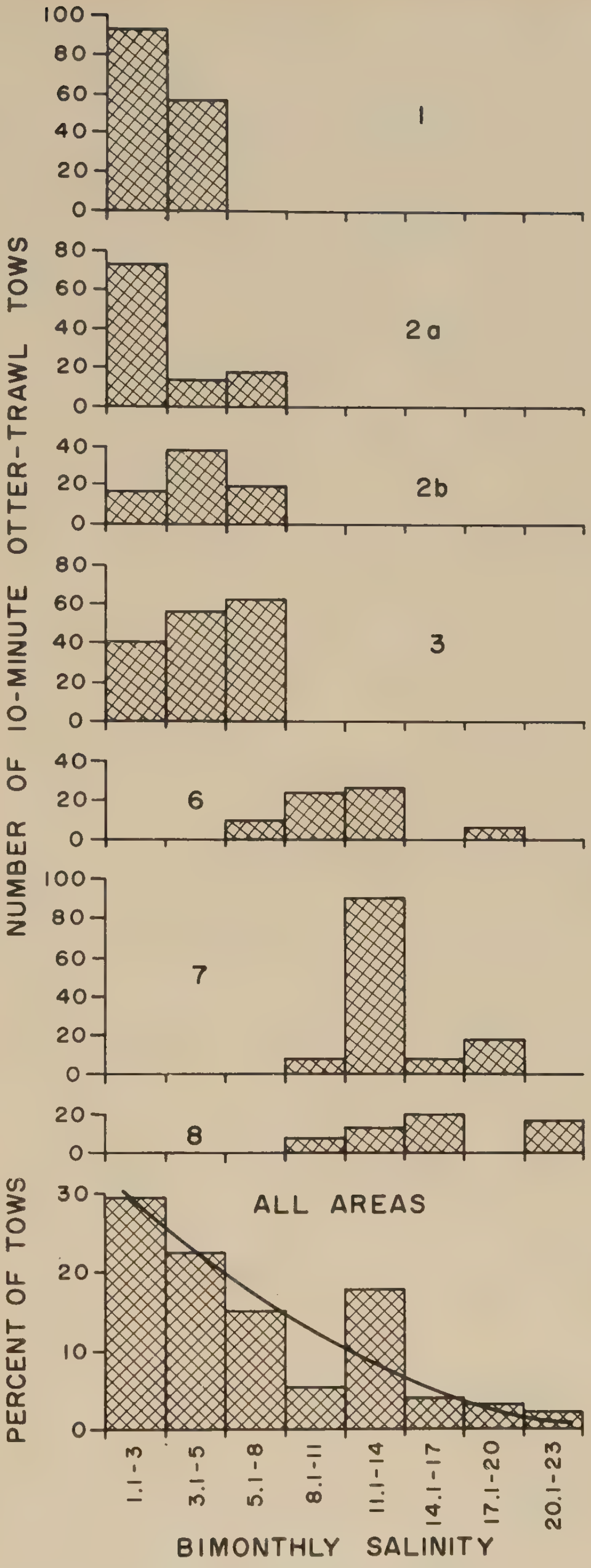

FIGURE 8.—Number of 10-minute otter trawl tows by the area and prevailing bimonthly salinity. The lower salinity sites are heavily oversampled.

GEAR

Several types of biological sampling gear were employed, but only the otter trawl could be called successful. The net measures 200 inches (16⅔ feet) across the headrope and 212 inches (17⅔ feet) along the footrope. The all cotton net has 9-thread 1¼-inch mesh, stretched measure, except for the cod end which has 12-thread 1⅛-inch mesh. The otter boards measure 10½ inches vertically by 24 inches horizontally by 1 inch in thickness with a steel reinforcing strap along the front and bottom edges. The boards were fastened directly to the ends of the wings. A galvanized iron chain, 13 links to the inch, and 18 feet long was suspended from the footrope. Four 3½-inch corks were attached to the headrope. The net was towed by two 75 foot lengths of ⅝-inch manila rope attached to a single warp.

A small net, described as a try net, was also used. It consisted of a triangle of ⅛ inch mesh nylon netting, 3 feet across the bottom in front, and attached to a 1½-inch, 3-foot length of galvanized pipe. The catch consisted chiefly of slow-moving forms such as larval and very small juvenile fishes. Catches were insufficient for making any quantitative analysis.

A larger cone of the same description was used in two ways; either attached to a 6-foot length of 2⅜-inch galvanized pipe, or attached to a rectangular pipe frame about 4½ feet wide and 13 inches high mounted on runners. Neither gear was used enough to provide sufficient material for analysis.

The small dredge used to collect mollusks had a mouth opening of only 16 inches. The bag was ¼-inch wire screen. The dredge when new had long teeth soldered onto the front blade. Through use the teeth were completely worn away, thus seriously biasing any quantitative comparisons.

Plankton tows were taken with a ½-meter net, but plankton volumes were not measured.

EFFECT OF SALINITY ON FISH DISTRIBUTION

One simple basis for predicting changes in fauna that might occur with any major changes in salinity is to determine the ranges of salinity in which various species of fish are found in reasonable numbers. The numbers of each species caught by otter trawl are shown in table 9. The numbers taken in each area are influenced by the number of tows made. To discount this variable, the total number of each species taken was distributed between areas on the basis of the number of tows. This gives the "expected" number that would be caught if tows alone were the deciding factor (ignoring for the moment, because of the paucity of sampling and low number involved, such other factors as seasonal occurrence). Determining the ratio of the observed to this expected number in each area and then comparing the ratios for all areas gives a rough measure of the areal distribution of each species.

The resulting relative abundance in numbers of all species of which 20 or more were taken by otter trawl is shown by area in table 10 and figure 9. The lack of samples from hydrographic areas 4 and 5 leaves a gap between the low salinity areas 1 to 3 and the higher salinity areas 6 to 8. It is quite obvious, however, that several species are confined to waters of low salinity; others to waters of higher salinity; with a larger number of species lying between that can apparently tolerate a fairly wide range of salinity.

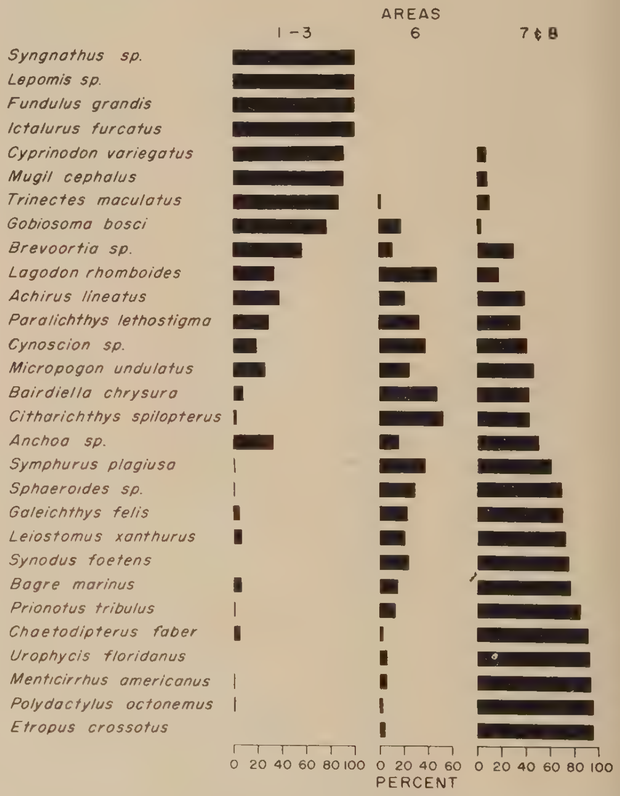

FIGURE 9.—Relative density of 29 species of fish in waters of low (areas 1–3), medium high (area 6), and high salinity (areas 7 and 8).

TABLE 9.—*Fish taken by otter trawl shown by species and area of capture*

[Number of fish]

Common name	Scientific name	Area of capture							
		1	2a	2b	3	6	7	8	Total
Spot	Leiostomus xanthurus	175	425	694	669	855	2,163	1,533	6,514
Croaker	Micropogon undulatus	547	1,518	581	320	375	449	311	4,101
Anchovy	Anchoa sp	515	853	511	529	166	156	361	3,091
Sea trout	Cynoscion sp	147	179	167	57	150	135	73	908
Blue catfish	Ictalurus furcatus	629	2	3	1	0	0	0	635
Sunfish	Lepomis sp	5	0	0	722	0	0	0	727
Hogchoker	Trinectes maculatus	206	258	46	35	2	8	4	559
Menhaden	Brevoortia sp	237	172	18	73	13	9	26	548
Sea catfish	Galeichthys felis	26	85	16	10	78	217	100	532
Fringed flounder	Etropus crossotus	0	0	0	0	11	133	146	290
Pinfish	Lagodon rhomboides	3	155	10	25	35	18	3	249
Spotfin whiff	Citharichthys spilopterus	2	22	9	2	83	57	34	209
Striped sole	Achirus lineatus	32	71	30	17	11	20	8	189
Eight-fingered threadfin	Polydactylus octonemus	0	4	12	0	4	65	86	171
Gulf killifish	Fundulus grandis	2	0	0	157	0	0	0	159
Puffer	Sphaeroides (3 species)	0	1	2	0	30	95	19	147
Silver perch	Bairdiella chrysura	7	8	17	21	42	29	19	143
Gafftopsail catfish	Bagre marinus	2	0	25	11	13	46	32	129
Sea robin	Prionotus tribulus	3	3	4	1	13	40	57	121
Spadefish	Chaetodipterus faber	2	2	2	8	1	20	22	57
Southern flounder	Paralichthys lethostigma	10	8	5	16	6	6	3	54
Lizardfish	Synodus foetens	0	1	0	0	9	23	11	44
Sheepshead minnow	Cyprinodon variegatus	1	0	0	41	0	1	0	43
Striped mullet	Mugil cephalus	2	0	0	39	0	1	0	42
Pipefish	Syngnathus sp	3	1	3	29	0	0	0	36
Naked goby	Gobiosoma bosci	4	2	1	27	1	1	0	36
Tonguefish	Symphurus plagiusa	0	1	0	0	11	13	11	36
Southern hake	Urophycis floridanus	0	0	0	0	2	13	19	34
King whiting	Menticirrhus americanus	1	0	0	0	1	12	9	23
Sheepshead	Archosargus probatocephalus	2	3	3	8	1	0	0	17
Threadfin shad	Dorosoma petenense	7	0	0	0	0	1	8	16
Cutlassfish	Trichiurus lepturus	0	0	1	0	2	8	5	16
Stingray	Dasyatis sabina	0	0	0	1	4	4	3	12
Sharp-tailed goby	Gobionellus hastatus	0	0	0	2	1	5	2	10
Toadfish	Opsanus beta	0	0	0	4	1	4	0	9
Miscellaneous species		22	3	4	27	12	12	26	106

TABLE 10.—*Relative abundance of principal species of fish according to areas taken*

Species	Areas			
	1–3	6	7	8
Ictalurus furcatus	100.0	0.0	0.0	0.0
Lepomis sp	100.0	.0	.0	.0
Fundulus grandis	100.0	.0	.0	.0
Syngnathus sp	100.0	.0	.0	.0
Cyprinodon variegatus	91.5	.0	8.5	.0
Mugil cephalus	91.3	.0	8.7	.0
Trinectes maculatus	87.6	2.4	4.7	5.3
Gobiosoma bosci	78.5	18.2	3.3	.0
Brevoortia sp	58.7	11.5	4.3	25.5
Achirus lineatus	39.9	21.6	20.9	17.6
Lagodon rhomboides	35.0	47.6	12.9	4.5
Paralichthys lethostigma	30.4	33.8	18.9	16.9
Micropogon undulatus	27.7	26.0	21.9	24.4
Cynoscion sp	19.8	39.4	19.0	21.8
Anchoa sp	33.1	16.9	8.4	41.6
Bairdiella chrysura	8.3	48.0	18.0	25.7
Citharichthys spilopterus	3.1	53.2	19.3	24.4
Symphurus plagiusa	.4	38.4	22.7	38.4
Galeichthys felis	5.7	23.9	35.4	34.9
Sphaeroides sp	.4	29.9	49.2	20.5
Leiostomus xanthurus	6.7	21.3	28.5	43.5
Synodus foetens	.3	24.4	35.6	39.7
Bagre marinus	6.6	15.8	30.6	46.9
Prionotus tribulus	1.6	13.2	21.3	63.9
Menticirrhus americanus	.9	6.2	37.2	55.8
Chaetodipterus faber	5.3	2.9	28.7	63.1
Urophycis floridanus	.0	7.3	23.7	69.0
Polydactylus octonemus	1.6	3.1	25.5	69.9
Etropus crossotus	.0	4.4	28.6	67.0
Bimonthly salinity (see table 7):				
Low	1.28	6.96	9.50	10.70
High	6.46	13.86	19.96	21.66
Average	3.48	11.61	14.98	16.96

In figure 9, an attempt has been made to rank the species of fishes in order of their preference from low to high salinity as shown by their relative abundance in the areas depicted.

That errors can easily creep into this type of reasoning is illustrated by the fact that *Mugil cephalus* and *Brevoortia* sp. appear from the figure to be most abundant in waters of low salinity. Actually, this is possibly the case for the juveniles, which were easily captured in the small mesh trawl, but not true for the adults, which could usually escape the trawl. Barring such unusual circumstances, the order of ranking probably represents a fair approximation of the relative effect of salinity on the abundance of these species.

In considering further the subject of salinity tolerance it will be noted from table 9 that no *Lepomis* sp. or *Fundulus grandis* were taken in Lake Borgne (areas 2a and 2b). All but a very few were taken at the stations in area 3 (BM, BG, and JDY). Their occurrence at these stations was highly erratic; 146 out of 159 *Fundulus* were captured in a single haul. This causes me to speculate that these two predominately fresh-water species were living chiefly in some of the diked marsh areas; some occasionally escaping into the surrounding bayous, the salinity of which, during portions of the year, could be tolerated by them.

FISH DENSITY BY AREA

An important question is how productive in finfish were the areas with different salinity levels. To answer this I show in table 11 the catch per tow in numbers and in biomass of five selected species, namely, spot, croaker, anchovy, sea trout, and menhaden. These five species were selected because of their widespread distribution, their high level of abundance, and their economic importance. Although the anchovy is not utilized directly, it is by far the most important forage fish in the area. Out of 20,013 trawl-caught fish (table 9), 15,162 or 76 percent belonged to this selected group.

Table 11.—*Number and biomass of selected fishes by area and season* [1]

Date	1 and 2a	2b and 3	6	7 and 8	Sum
	Biomass per tow (in grams)				
1959					
October-November	190.3	61.9	242.9	204.0	699.1
December-January	140.0	20.0	130.4	39.0	329.4
1960					
February-March	77.7	12.9	21.8	5.9	118.3
April-May	210.3	218.6	184.6	351.0	964.5
June-July	120.4	406.6	504.7	431.8	1463.5
August-September	148.6	58.4	53.4	442.9	703.3
October-November	113.4	162.8	336.0	308.5	920.7
December-January	306.0	55.8	183.9	399.0	944.7
1961					
February-March	130.4	101.3	204.1	162.9	598.7
Average	159.7	122.0	206.9	260.6	--------
	Numbers per tow (5 cm. and over in length)				
1959					
October-November	12.5	2.4	15.2	9.6	--------
December-January	5.3	0.8	7.6	1.5	--------
1960					
February-March	13.7	1.7	2.6	1.5	--------
April-May	41.6	42.0	28.0	73.2	--------
June-July	17.5	38.1	78.8	56.1	--------
August-September	6.6	4.8	3.4	32.4	--------
October-November	5.9	8.5	16.0	12.9	--------
December-January	14.3	3.6	10.3	16.9	--------
1961					
February-March	15.7	9.8	13.8	12.5	--------
Average	14.8	12.4	19.5	24.1	--------

[1] Includes spot, croaker, anchovy, sea trout, and menhaden.

The numbers of fish per tow in table 11 are those of individuals 50 mm. or more in length. Smaller fish were captured in all areas, but because of the selectivity of the otter trawl mesh they were not captured consistently and so have been omitted.

The biomass per tow could only be obtained by estimation from the lengths of the fish, as weights were not taken. From length-weight data collected by C. R. Mock in Galveston Bay it was possible to estimate roughly what individual fish in each 5-cm. category should weigh during each 2-month period. The rough estimate of individual weight used in grams is:

Mouths	Fish lengths (cm.)			
	0–5	6–10	11–15	16 and more
February-March	1	2	27	74
April-May	1	4	24	70
June-July	1	6	15	66
August-September	1	9	18	55
October-November	1	12	21	66
December-January	1	12	24	72

In figure 10 are shown the estimated biomass (top) and the numbers of fish of 5 cm. and over (bottom), by area and bimonthly period. In both numbers and biomass the Lake Borgne and adjacent areas (1 through 3) were less productive than areas 6 through 8.

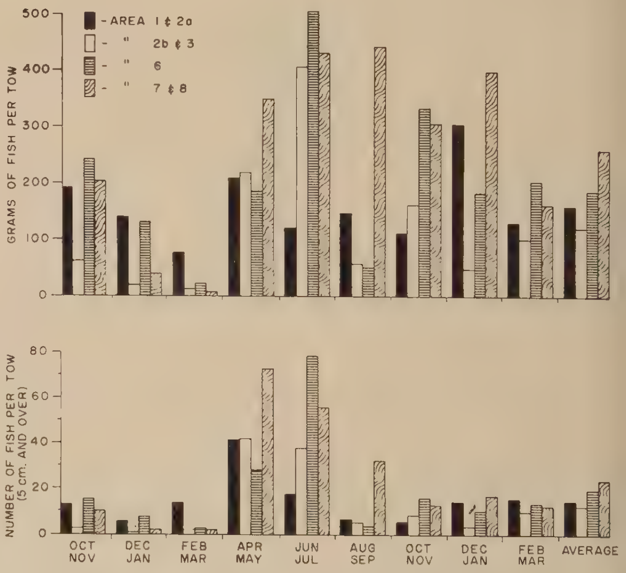

Figure 10.—Numbers and biomass of five selected species of fish by area and season.

CRUSTACEA

Enumerations and measurements were made of brown, white, and pink shrimp, and of blue crabs taken in the otter trawl samples. Only 122 pink shrimp were recorded; all were taken during the last 6 months of the 24-month period. One may speculate that during the earlier months more may have been caught that were classified as brown shrimp.

Out of 9,187 shrimp of all sizes taken, only 419 under 50 mm. were retained by the otter trawl, or 4.6 percent. By contrast 3,059 out of 5,200 blue crabs, or 58.9 percent were under 50 mm. The catch per unit of sampling effort for shrimp of 50 mm. and over is shown in table 12 and in figure 11 for the 18-month period from October 1959 to March 1961. In contrast with the white shrimp, few brown shrimp over 100 mm. were caught. This reflects the Gulf-wide behavior of brown shrimp, which leave the protected waters for the Gulf at a smaller size than do the white shrimp.

There appears to be little salinity preference. Brown shrimp below 100 mm. were taken in all areas. White shrimp below 100 mm. were abundant in three areas, but very scarce in the open waters of Lake Borgne, and only moderately abundant in the rather open waters of areas 7 and 8. Young white shrimp thus appear to prefer shoal, protected waters.

Shrimp are transient residents of the marsh areas. Figure 12 shows the bimonthly catch per 10 tows of white and brown shrimp 50 mm. and over. From December through March, shrimp are almost nonexistent in the areas. Brown shrimp appear in April and May and quickly increase in numbers. By the end of July the numbers of brown shrimp are falling rapidly as the larger sizes emigrate to the Gulf. The peak of abundance for white shrimp comes from 1 to 2 months later.

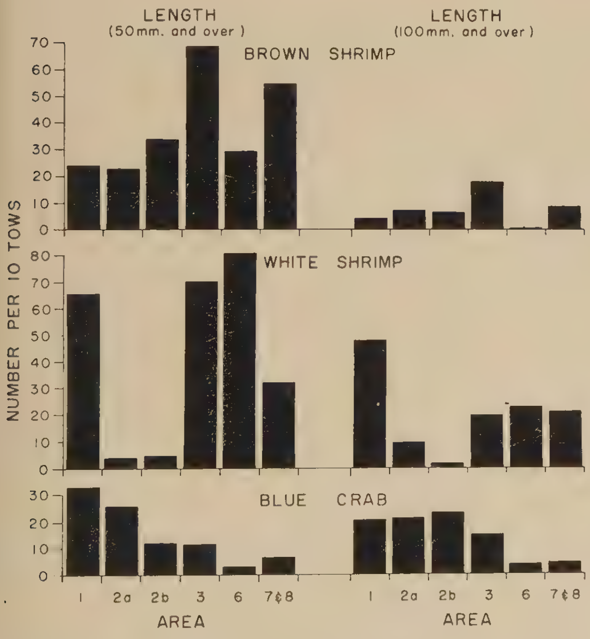

FIGURE 11.—Average catches by size of brown and white shrimp, and blue crabs, per 10 tows by area for the 18-month period, October 1959 to March 1961.

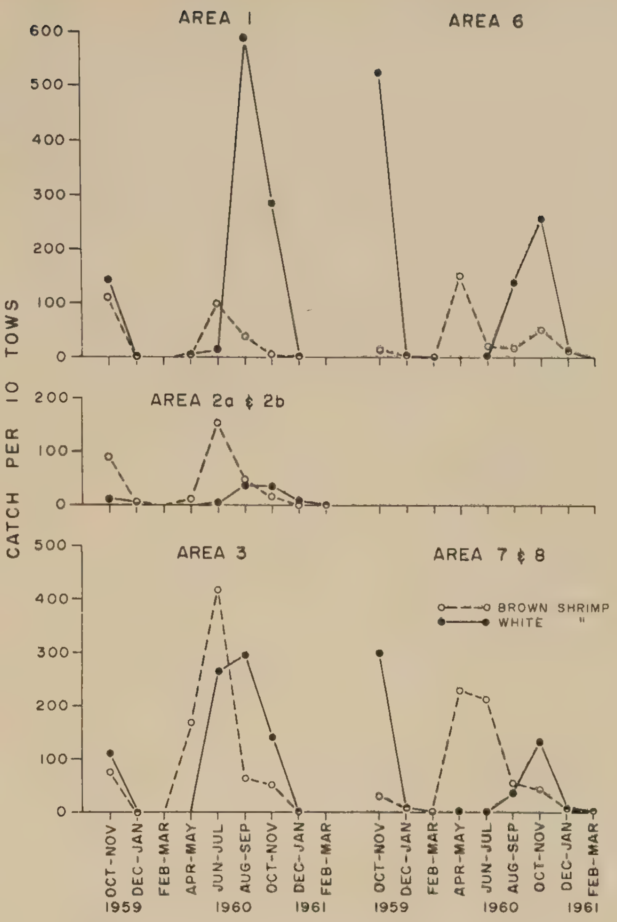

FIGURE 12.—Catches of brown and white shrimp per 10 tows by area and bimonthly period.

Blue crabs between 50 and 100 mm. (fig. 11) became progressively less abundant as salinity increased. The larger blue crabs (100 mm. and over) were about equally abundant in all of the areas bordering Lake Borgne, but like the smaller sizes they were scarce in areas 6 through 8. Mature female crabs are known to migrate considerable distances in a matter of a few days to reach higher salinity water for spawning (Fiedler, 1930). Salinities ranging from 23°/oo to 30°/oo were found by experiment to be optimal for hatching of blue crab eggs (Sandoz and Rogers, 1944). To

TABLE 12.—*Number of shrimp caught per 10 tows of an otter trawl*

Date	Area											
	1		2a		2b		3		6		7	8
	Length of shrimp (millimeters)											
	50–99	100 and more	50–99	100 and more	50–99	100 and more	50–99	100 and more	50–99	100 and more	50–99	100 and more
	BROWN SHRIMP											
1959												
October–November	111.7	--------	53.3	--------	121.7	3.3	76.4	2.2	16.7	--------	30.0	1.1
December–January	1.7	--------	0.6	--------	1.3	--------	0.8	--------	1.3	--------	7.5	--------
1960												
February–March	--------	--------	--------	--------	--------	--------	--------	--------	3.3	--------	2.9	--------
April–May	6.6	--------	3.3	--------	17.5	0.9	166.5	1.1	151.7	--------	226.3	2.9
June–July	71.7	25.6	94.2	38.3	127.5	46.7	288.8	129.6	21.7	--------	173.9	38.3
August–September	26.7	10.7	36.0	26.0	27.1	5.7	44.0	20.0	18.0	--------	20.0	33.5
October–November	2.5	2.5	21.3	1.3	8.8	1.3	40.0	12.5	47.5	2.5	36.9	3.8
December–January	0.8	0.8	--------	--------	2.5	--------	3.3	--------	7.5	--------	3.0	--------
1961												
February–March	--------	--------	--------	--------	1.3	--------	--------	--------	--------	--------	0.5	--------
Average	24.6	4.4	23.2	7.3	34.2	6.4	68.9	18.4	29.7	0.3	55.7	8.8
	WHITE SHRIMP											
1959												
October–November	93.9	50.6	8.3	--------	11.7	3.3	77.5	34.3	508.3	16.7	232.2	64.3
December–January	0.9	--------	1.3	--------	1.3	--------	--------	--------	3.8	--------	3.8	--------
1960												
February–March	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------
April–May	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	0.8	--------
June–July	16.1	0.6	9.2	1.7	5.0	--------	262.0	3.9	1.7	--------	0.9	--------
August–September	365.3	223.3	12.0	45.0	17.1	4.3	236.0	60.0	98.0	40.0	11.8	23.5
October–November	118.3	163.3	6.3	41.3	10.0	8.8	56.7	85.0	107.5	152.5	30.6	102.5
December–January	--------	--------	1.3	--------	--------	--------	1.7	--------	10.0	--------	9.5	--------
1961												
February–March	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	2.0	1.5
Average	66.1	48.7	4.3	9.8	5.0	1.8	70.4	20.4	81.0	23.2	32.4	21.3

reach water of such salinity the female crabs in the project area would need to move at least as far as either Chandeleur Sound or Mississippi Sound. Darnell (1959) collected spawning females in Chandeleur Sound and the eastern end of Lake Borgne in a salinity range of 19.2°/₀₀ to 31.5°/₀₀.

Pearson (1948) says that the young blue crabs hatched in Chesapeake Bay begin to migrate toward brackish water and that this migration, halted by cold weather, is resumed in the spring. In the project area (table 13) crabs under 50 mm. are most abundant in winter (December through March). This difference between localities may be caused by the milder southern winters.

Since small blue crabs (under 50 mm.) were retained in large numbers by the otter trawl it is possible to arrive at some estimate of their abundance seasonally and by area (table 13 and figure 13). These very small crabs (under 50 mm.) are most abundant in the winter and early spring and extremely scarce from June through September. They are abundant in the open (and low salinity) waters of Lake Borgne, and scarce in the semi-open (and moderately high salinity) waters of areas 6 to 8. Although crabs of this small size were not particularly abundant in areas 1 and 3, the slightly larger crabs (50–99 mm.) were more abundant in the low salinity waters of area 1 than in Lake Borgne. This seems to indicate a migration of these smaller crabs toward shallow and low salinity areas as they grow.

SUMMARY OF BIOLOGY

1. Only the otter trawl samples are sufficiently extensive and consistent to warrant quantitative treatment.

2. Lack of samples in areas of intermediate salinities (areas 4 and 5) precludes any precise conclusions regarding the effect on the fauna of salinity changes.

3. The bulk of the fish species taken were euryhaline. This included the species caught in greatest abundance.

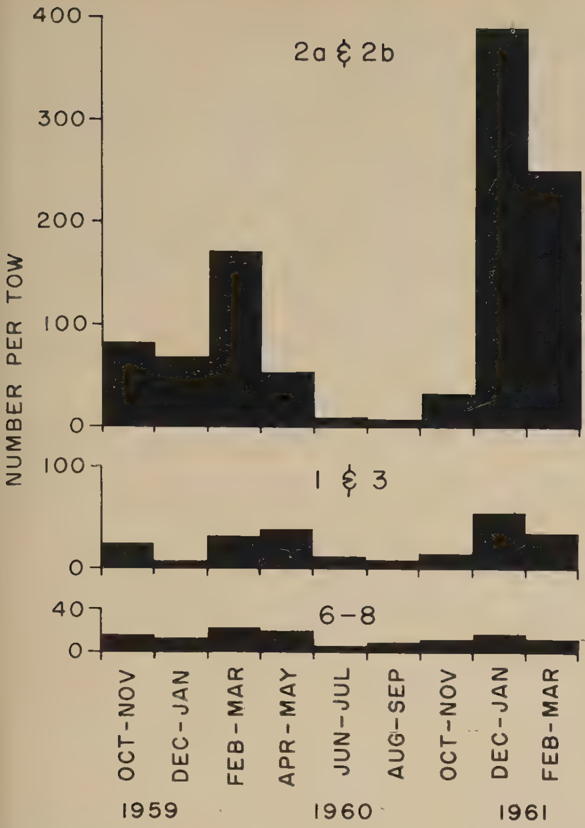

FIGURE 13.—Catches of very young blue crabs (under 50 mm.) by area and bimonthly period.

4. Seventy-six percent of the fish taken were of only five species.

5. In both numbers and biomass these five species were more abundant in areas 6 to 8 than in areas 1 to 3.

6. Neither brown nor white shrimp showed any significant salinity preference.

7. Smaller white shrimp were less abundant in open waters than in the shoal marshes.

8. From December through March shrimp are almost absent from the project area.

9. Smaller blue crabs (50 to 100 mm.) were most abundant in area 1 decreasing progressively to area 3; they were scarce in areas 6 through 8.

10. Larger blue crabs (100 mm. and larger) were about equally abundant throughout areas 1 to 3; but scarce in areas 6 through 8.

DISCUSSION

The Gulf outlet channel will apparently have some effect on the hydrography of the project area. Most probably the chief effect will be a raising of the salinity. This may be accomplished in three ways, first, by mixture of channel water with that of the surrounding bayous through intersection points. Secondly, by raising of the salinity in Lake Pontchartrain through movement of the denser and more saline water from the deeper layers of the channel into the lake. The higher salinities in Lake Pontchartrain would in turn raise salinities in Lake Borgne. The third means of raising salinities would be through the effect of the occasional abnormally high tides which would

TABLE 13.—*Number of blue crabs caught per 10 tows of an otter trawl*

Date	Area																	
	1			2a			2b			3			6			7 and 8		
	Length of crabs (millimeters)																	
	0–49	50–99	100 and more	0–49	50–99	100 and more	0–49	50–99	100 and more	0–49	50–99	100 and more	0–49	50–99	100 and more	0–49	50–99	100 and more
1959																		
October–November	37.2	31.7	12.8	88.3	53.3	3.3	73.3	6.7	23.3	11.2	12.9	22.5	8.3	1.7	5.0	23.5	2.2	3.3
December–January	13.0	24.8	2.2	108.4	7.1	19.5	27.5	13.8	37.5	2.8	21.7	19.3	11.3	------	------	12.5	5.6	1.9
1960																		
February–March	62.1	13.8	1.1	321.3	5.6	8.8	20.0	------	6.0	3.2	3.7	3.2	3.3	------	------	44.3	2.5	0.7
April–May	39.8	46.4	15.7	61.7	25.8	21.7	45.5	21.8	20.0	37.4	14.5	20.1	6.7	5.0	1.7	32.9	15.8	4.2
June–July	7.8	21.7	16.7	4.2	21.7	21.7	10.0	21.7	21.7	17.3	8.9	7.3	5.0	15.0	10.0	1.7	7.0	7.0
August–September	8.7	34.0	29.3	8.0	34.0	49.0	1.4	2.9	24.3	7.3	12.0	6.7	10.0	2.0	8.0	------	6.5	5.3
October–November	24.2	42.5	39.2	23.8	17.5	30.0	40.0	11.3	20.0	7.5	10.8	27.5	17.5	5.0	10.0	6.9	14.4	10.0
December–January	81.7	34.2	22.5	613.8	23.8	13.8	165.0	23.8	36.3	26.7	14.2	20.8	27.5	2.5	2.5	4.0	6.5	2.5
1961																		
February–March	55.0	50.0	48.3	277.5	46.3	27.5	227.5	11.3	22.5	14.2	10.8	10.0	15.0	2.5	------	10.5	2.0	6.5
Average	36.6	33.2	20.9	167.4	26.1	21.7	67.8	12.6	23.5	14.2	12.2	15.3	11.6	3.7	4.1	15.1	6.9	4.6

be heightened by the close proximity of highly saline water in the channel.

The effect of the Gulf outlet channel on the salinity in Lakes Pontchartrain and Borgne has been studied in a large model at the Waterways Experiment Station, Vicksburg, Miss. The fishery aspects of these experiments have been reported upon by the Bureau of Sport Fisheries and Wildlife.[3]

This report shows that salt-water intrusion in the Gulf outlet channel will be severe. With the outlets to Lake Pontchartrain partially closed by hurricane protection structures but with no control in the Gulf outlet channel the model indicates (their figure 3) a rise in Lake Pontchartrain salinity of about 4.3°/₀₀ in years of high fresh-water inflow and about 5.5°/₀₀ for years of low inflow. The model indicates that this condition can be considerably corrected by placing control structures in the Gulf outlet channel where it intersects the Industrial Canal.

Heightened salinities in Lake Pontchartrain will in turn raise salinities in Lake Borgne by 1°/₀₀ to 2°/₀₀. However, the marsh lying between Lake Borgne and the channel instead of being dominated by Lake Borgne will now have direct and easy access to the waters of the Gulf. Thus the model studies indicate that under the best conditions of control of channel flow into Lake Pontchartrain (lowest salinities occurred in the model when channel flow was 60 percent of capacity) the salinity in the channel at a point close to station BWA was about 12°/₀₀ at a depth of 6 feet and about 26°/₀₀ at a depth of 12 feet.

Obviously, this marsh area (1 and 3) with a preproject salinity of about 2°/₀₀ to 5°/₀₀ is due for a pronounced rise in salinity.

The portions of the project area lying south of the channel will also experience a rise in salinity. Before the project, water from Lake Borgne and from Breton Sound was exchanged through the bayou systems resulting in the long-term salinity gradients shown in figure 5. With the project completed, water from Lake Borgne can reach this southerly portion of the project area only by crossing the wide channel at the few intersection points. Obviously, the future exchange of Lake Borgne water with the water south of the channel will be very limited, and it will be mixed with channel water. Therefore, the areas southwest of the channel may be expected to experience a rise in salinity to a level higher than the portions of the project area between the channel and Lake Borgne.

Since the channel extends entirely across Breton Sound into the open Gulf the channel may have some elevating effect on the salinities in Breton Sound itself.

It is too soon to predict the final salinity changes engendered by the project, but it would appear that salinities in the project area with the optimum control of exchange at the northern end of the Gulf outlet channel will rise about 2°/₀₀ in Lake Borgne and at least 5 or more parts per thousand in the remainder of the project area.

The effect on the vertebrate fauna of such a rise in salinity will not necessarily be drastic. The principal species of fish in the area are obviously euryhaline, and of the remaining species, the majority are more adapted to higher than to lower salinities.

The brown shrimp shows no obvious salinity preference. The salinity preference of the white shrimp is somewhat obscured by the fact that the smaller juveniles apparently avoid the more open waters in favor of the shoal, protected marshes. On the whole the white shrimp may suffer some loss of what has been desirable nursery area, especially where the salinity rises appreciably above the 14°/₀₀ isohaline now separating areas 6 and 7.

The younger stages of the blue crab are now most abundant in the least saline waters (area 1), decreasing progressively and significantly as salinity increases toward area 3. Both young and adult crabs are scarce in areas 6 to 8. A rise in salinity should have an adverse effect on the abundance of crabs.

It is highly probable that a general rise in salinity will seriously affect the growing of oysters. Oyster beds, especially those used for collecting seed oysters, can be extensively harmed by only a slight rise in salinity, especially if it occurs when the salinity is at the borderline between suitability and unsuitability for oyster drills. Conversely, a rise in salinity may make some areas suitable for oyster growing where previously the average salinities have been consistently too low for successful oyster culture.

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[3] A detailed report on Hurricane Study Area No. 1: Lake Pontchartrain and vicinity, Louisiana. 32 p., 1 map, 9 figs., processed (issued in 1962 by Region 4, Bureau of Sport Fisheries and Wildlife, Atlanta).

The idea that a possible benefit could offset damage to existing oyster beds is highly speculative.

In evaluating losses attributable to the project one must consider the value of the areas occupied by the channel and the resulting spoil. The Branch of River Basin Studies of the Bureau of Sport Fisheries and Wildlife has furnished careful measurements of these areas:

Acres occupied by the project

Original state	Channel	Spoil areas	Total
Open water	1,680	4,518	6,198
Marsh	4,868	12,540	17,408
Total	6,548	17,058	23,606

The above tabulation of project area between the Intracoastal Waterway and Breton Sound shows that it occupies 23,606 acres or 36.9 square miles. The portion originally designated as marsh includes such shallow marginal areas as are occupied by emergent vegetation. Much of the remainder of the marsh is under water during extreme tides, which occur especially during late summer. Thus, in addition to the 6,198 acres of open water a fair portion of the 17,408 acres of marsh must be considered as nursery area for shrimp, crabs, and juvenile fishes.

Since the channel itself will be open water (6,548 acres), there will be little change in the total surface of open water. However, the preproject open water consists of many shallow winding bayous that provide a very long shoreline adjacent to emergent vegetation—an ideal nursery area. The postproject open water is a deep channel along which the greatly reduced shoreline will be subjected to the constant wash of passing traffic. The shallow portions of the "marsh" areas bordering the bayous will be totally lost in the spoil areas.

The above losses of nursery habitat are permanent and irreplaceable.

It should be borne in mind that the effect of the project on the remainder of the area is not merely a narrowing of the coastwise belt of low salinity water. Such a situation would merely push the belt of marsh suitable for juvenile fauna farther inland. Instead, the channel carries saline water far inland so that Lake Pontchartrain will have higher salinity than Lake Borgne. Thus, fauna seeking to remain in the same salinity now prevailing in a large portion of the project area have lost the former bordering area of low salinity to which they could retreat.

This report is concerned wholly with the effect of the Gulf outlet channel on the commercial fisheries of the project area. The effects of salinity changes on the vegetation and directly or indirectly on waterfowl and furbearers is not touched upon.

LITERATURE CITED

Darnell, Rezneat M.
1959. Studies of the life history of the blue crab (*Callinectes sapidus* Rathbun) in Louisiana waters. Transactions of the American Fisheries Society, vol. 88, No. 4, p. 194–304.

Fiedler, R. H.
1930. Solving the question of crab migrations. Fishing Gazette, vol. 47, No. 6, p. 18–21.

Marvin, Kenneth T., Zoula P. Zein-Eldin, Billie Z. May, and Larence M. Lansford.
1960. Chemical analyses of marine and estuarine waters used by the Galveston Biological Laboratory. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 349, 14 p.

Pearson, John C.
1948. Fluctuations in the abundance of the blue crab in Chesapeake Bay. U.S. Fish and Wildlife Service, Research Report 14, 26 p.

Sandoz, Mildred, and Rosalie Rogers.
1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab, *Callinectes sapidus*, Rathbun. Journal of Ecology, vol. 25, No. 2, p. 216–228.

A MORPHOMETRIC STUDY OF YELLOWFIN TUNA *THUNNUS ALBACARES* (BONNATERRE)

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ABSTRACT

Morphometric measurements were compared for 4,180 yellowfin tuna from 28 locations in the Pacific Ocean; from off Angola, Africa, in the Atlantic Ocean; and from off Somaliland, Africa, in the Indian Ocean. The measurements used were head length; pectoral fin length; heights of second dorsal and anal fins; distances from snout to insertion of first dorsal fin, to second dorsal fin, anal fin, and ventral fin; distance from insertion of ventral to anterior edge of vent; and greatest body depth. Each measurement was related to fork length by regression analysis, and each relationship was considered a character. Curvilinear regression due to allometric growth was controlled by transforming some data to logarithms and by separating all samples into small, medium, and large size groups (less than 80, 80–120, and greater than 120 cm. fork lengths). Mean character sizes were determined for each sample at lengths of 65, 100, and 140 cm.

A comparison of mean character sizes revealed a cline in most characters from samples taken along the Pacific Equator between the vicinity of Costa Rica and the Caroline Islands. Yellowfin from the eastern Pacific have larger heads and greater distances from snout to insertion of first dorsal, second dorsal, ventral, and anal fins; a greater distance from insertion of ventral fins to insertion of anal fin; and a greater body depth. On the other hand, they have shorter pectoral fins and much shorter anal and second dorsal fins. The samples from the more temperate parts of the Pacific and from off the coasts of Africa differed little from some part of this cline.

A multiple character comparison of overlap among samples from near the Pacific Equator showed less than 50-percent overlap between samples separated by 1,500 miles, less than 25-percent overlap between samples separated by 3,000 miles, and less than 6-percent overlap between samples separated by 6,000 miles. The possibility of long intermigrations among the equatorial stocks seems remote.

The full variation in length of the pectoral fin and heights of second dorsal and anal fins, which most authors have used to separate the species of yellowfin, occurs within the cline along the Pacific Equator. This occurrence, plus the continuous circumtropical high seas distribution of the yellowfin, indicates a single worldwide species. The appropriate name is *Thunnus albacares* (Bonnaterre) 1788.

A problem of immediate concern to us in investigation of the tuna fisheries of the Pacific is to determine the degree of intermingling of the tuna populations. Intermingling matters because tunas are being sought in different parts of the ocean by fishermen who are asking whether the catch by one nation in one area is affecting the population of tunas and catch by another nation in another area. In other words, do these tunas migrate thousands of miles, as do some of our migratory birds, or are they relatively localized, hatching, maturing, and dying within an area of a few hundred miles? A closely related matter of secondary concern is to distinguish the species and subspecies of each kind of tuna in the oceans of the world.

Among the tuna fisheries of the Pacific, those for the yellowfin (*Thunnus albacares*) [1] are the most

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Note.—Approved for publication June 3, 1963.

[1] The Pacific yellowfin tuna has been named *Neothunnus macropterus* (Temminck and Schlegel) by recent authors. I consider the yellowfin to be a single worldwide species, which I choose to call *Thunnus albacares* (see page 428).

important. The yellowfin is a major fishery resource from California to Chile and from Japan to Indonesia, especially near the Caroline Islands. Smaller fisheries also exist off Hawaii, Australia, and many of the islands of the central Pacific. In addition, exploration by the Bureau of Commercial Fisheries Pacific Oceanic Fishery Investigations (POFI) [2] in the central Pacific revealed major concentrations of yellowfin along the Equator from longitude 110° W. to 180°. These stocks were fished repeatedly by research vessels and subsidized commercial vessels between 1950 and 1955. The methods and results have been summarized by Sette (1954) and detailed by Murphy and Shomura (1953a, 1953b, and 1955) and Shomura and Murphy (1955). Since 1955 these populations have been fished with increasing intensity by Japanese commercial concerns.

One approach to the general problem of relations among Pacific tuna stocks has been through morphometric studies. Workers have included Schaefer (1948), who described the morphometric characteristics and relative growth of yellowfin off central America; Godsil (1948), who made a preliminary population study of yellowfin and albacore, *Germo alalunga* (Bonnaterre); Schaefer and Walford (1950), who compared yellowfin from off Angola, Africa, and the Pacific coast of Central America; Schaefer (1952), who compared yellowfin from the Hawaiian Islands with those from the Pacific coast of Central America; Royce (1953), who compared numerous groups of Pacific yellowfin; Tsuruta (1954), who compared yellowfin from the Gilbert Islands with those from Hawaii; and Schaefer (1955), who further compared yellowfin tuna from Central America and Hawaii with those of southeastern Polynesia.

A different technique, which may provide direct evidence of intermingling, has been applied by the California Department of Fish and Game, Marine Fisheries Branch, and used subsequently by other groups. Yellowfin, albacore, and skipjack, *Katsuwonus pelamis* (Linnaeus), have been tagged with plastic tags, as reported by Wilson (1953), and have already shown some remarkable migrations. One albacore released 18 miles south of Los Angeles, California, was recovered nearly 1 year later about 5,000 miles distant at latitude 31°30′ N., longitude 149°40′ E., off the coast of Japan (Ganssle and Clemens, 1953) and two other albacore, tagged near Guadalupe Island, were recovered about 6 months later in the vicinity of Midway Island (Blunt, 1954). Yellowfin also were tagged off the Line Islands from March 1955 to February 1956 (Iversen and Yoshida, 1957). Of the 1,056 that were released, 2 were recaptured locally and 1 was recovered 800 miles east of the point of release after being at liberty 13 months. But these tag returns are as yet too few to provide good evidence of the extent of intermingling or of any different migratory behavior of the several species.

Much interest in these problems of intermingling of tuna populations has been expressed at various meetings of the Indo-Pacific Fisheries Council, and the collection of data has been a matter of major concern to its Tuna Subcommittee. Through this organization the aid of numerous people in the Indo-Pacific area has been enlisted in the collection of data, which have been used in this report. This interest has also been expressed by some independent studies along the same lines in other countries, particularly in Japan by Tsuruta (1954) and in Australia where morphometric studies are underway.

STATISTICAL COMPARISON OF MORPHOLOGICAL DATA

The following section is a summary of a general review of the problem involved in statistical comparisons of morphological data previously made by Royce (1957).

In all morphometric studies of yellowfin tuna the authors have used essentially the same methods. All have used measurements of body parts, especially lengths and heights of the fins and distances from the snout to insertion of the fins, as principal characters. All have used regression analysis to relate part size to fork length and then have compared samples by covariance analysis. All have found much larger differences between samples than would be expected from chance variations, and from such differences there has been a tendency to conclude that the populations were distinct.

But this method of analysis is not wholly satisfactory. It provides a test of whether a difference is significant, but this conclusion may be trivial, because significant differences can be found commonly between even the most closely related natural populations (Mayr, Linsley, and Usinger, 1953: 151). It does not show how great the differences are in terms that can readily be compared. It does not provide evidence of clines or character gradients, which are to be expected in tuna populations because of their continuous distribution and which are useful indicators of relations of the populations. Neither do the methods in current use provide information on the key problem of the amount of intermingling.

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[2] Now the Biological Laboratory of the Bureau of Commercial Fisheries, Honolulu, Hawaii.

Use of regression analysis to relate size of body parts to fork length does provide basic data needed for finding clines according to the method described by Hubbs and Hubbs (1953). The regression statistics provide the mean character size estimated for a fixed length of fish; the measure of dispersion about the mean, which is the standard deviation from regression; and the measure of reliability, which is the standard error of the estimated mean. I showed that clines exist among yellowfin tuna populations (Royce, 1953), but I did not use the method of Hubbs and Hubbs nor employ sufficiently precise methods of regression analysis. In this paper I will use more refined methods of regression analysis and try to show fully the nature of the clines.

The problem of intermingling will be approached through an extension of the concept of overlap, which has been applied to comparison of natural populations by many taxonomists. The methods in current use have been summarized by Mayr, Linsley, and Usinger (1953: 142). They have indicated overlap between populations by a coefficient of difference (CD), which is computed according to the formula—

$$\mathrm{CD}=\frac{\bar{x}_1-\bar{x}_2}{s_1+s_2}$$

The overlap is the difference between means $\bar{x}_i$ divided by the sum of standard deviations s_i of the two populations. I prefer to change this formula slightly to—

$$D=\frac{\bar{x}_1-\bar{x}_2}{s}$$

in which s is the within-sample standard deviation computed from the pooled variance, and D is the distance between the means in the standard measure of statistics, i.e., in units of the standard deviation. It is obvious that $\mathrm{CD}\simeq\frac{D}{2}$.

The concept of overlap of two frequency distributions is shown graphically (1A and 2A) in figure 1. The mutual area (1B and 2B) of the two curves is shaded; one-half of the shaded area, or tail of one distribution, which I designate as p, may be determined readily from a table of the probability integral, such as table 2 in Pearson (1948). The table is entered with the value of $\frac{D}{2}$. The value of p represents the probability of misclassifying the individuals on the basis of the character used. When the two means are identical and the chances of making a proper choice are equal, p will range from 0.5 to essentially zero when the two curves are widely separated, and for all practical purposes there is no overlap. However, the value p, while indicative of overlap, is not fully satisfactory because it approaches a maximum of 0.5 and because it must be considered properly as a probability of misclassification rather than a measure of the mutual area of the frequency curves.

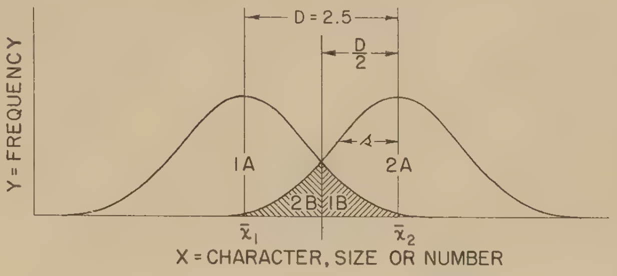

FIGURE 1.—Overlap of normal distributions. 1A and 2A indicate normal populations which overlap in the shaded areas 1B and 2B; s indicates one standard deviation, $\bar{x}_1$ and $\bar{x}_2$ indicate means; D is the distance between means in units of the standard deviation.

A more satisfactory measure of overlap may be obtained if one considers the area of one frequency curve and within it the proportion (2_p) that might belong to another specified frequency curve. I have designated this by $\Omega=200\ p$, expressed as a percentage. It is a measure of overlap which will be 100 percent when the curves have the same mean and will approach zero as the means become widely separated.

The particular usefulness of Ω is in the concept that it is an estimate of the proportion of one sample with the characteristics of another. If the samples are representative of populations in a specific time and place, it follows that Ω is that proportion which might have come from another population, and thus the value of the overlap indicates a maximum for the amount of intermingling. The overlap Ω does not show that intermingling has occurred, and when large it merely shows that a large amount of intermingling may have occurred. Whether intermingling did occur must be determined by other means. When Ω is small, however, and we can establish that the characters used do not change during migration, we may then be able to establish that no significant intermingling occurs.

The most satisfactory measure of overlap is obtained from several characters simultaneously, which requires a substantial extension of the computations. The measure in current use by most taxonomists has been applied merely to comparisons of single counted characters. I have shown (Royce, 1957) that it may be applied readily to single measured characters through substitution of the regression statistics. The much greater extension to multiple characters is based on *D* as already defined. The use of *D* as a distance between populations has been generalized for multiple characters by Mahalanobis (1936). In his generalization, each additional character adds to *D* only to the extent that it is not correlated with previously considered characters. Thus, all arbitrary combinations of characters as ratios or indices are avoided. Rao (1947, 1952) pointed out that *D* satisfies two fundamental postulates of distance: (1) the distance between two groups is not less than zero; (2) the sum of distances from one group to two other groups is not less than the distance between the two other groups (triangle law of distance). The further empirical requirement that the distance must not decrease when additional characters are considered is also satisfied.

AVAILABLE DATA

There were available for this study 28 samples of yellowfin from the Pacific Ocean, 1 from the Atlantic Ocean off Angola, Africa, 1 from the Indian Ocean off Somaliland in northeast Africa, and 1 of only 3 specimens from off Ceylon.[3] The data include the measurements of yellowfin from off the American coast published by Godsil (1948), whose 13 samples have been combined into 6; those from off Costa Rica by Schaefer (1948); from Angola by Schaefer and Walford (1950); from Fiji, Palmyra, and Hawaii by Godsil and Greenhood (1951); from Hawaii by Schaefer (1952); and those from the Gilbert Islands by Tsuruta (1954). The original measurements of most of the remaining samples were published by Dung and Royce (1953). The remainder, a sample from the Pacific Equator near longitude 110° W. and another from northeast Africa, are listed in appendix tables 1 and 2.

The geographic distribution of Pacific samples is shown in figure 2. There is an excellent series from about 8,000 miles along the Pacific Equator between the American coast and the central Caroline Islands. In addition, there are samples from the South Pacific off the Fiji and Society Islands, and from the North Pacific off the Philippines, Japan, Bikini Island, Hawaii, Mexico, and Guatemala. All major areas of the Pacific where yellowfin are known to occur are included except the South American coast and the southwest Pacific from Australia to the coast of Asia.

It was necessary to omit four samples from the Pacific. Those from the western Marshall, western Caroline, and Fiji Islands have not been further considered, because they contain less than 20 fish, the number I arbitrarily established as the minimum. In another sample from near the Gilbert Islands, reported by Tsuruta (1954), measurements of one specimen are questionable (No. 2 in his table 1), and I have been unable to verify the computations shown in his table 2. Fairly large discrepancies occur in the regression statistics, apparently because enough digits were not carried during the computations. This sample was obtained on only 3 days from a limited area. For these reasons I have not further considered it.

Certain basic statistics about the samples will be needed repeatedly in the ensuing discussion and are presented here. The length distribution of all samples is shown in table 1. Pertinent data on how the samples finally used were collected are shown in table 2. The sums, sums of squares, and sums of products for all characters of all samples which have not been published are given in appendix table 3. Included, also, are the means, regression constants, and estimated character sizes at certain lengths for all samples.

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[3] This sample was compared with the Pacific samples by Royce (1953) and found to be most like the Phoenix Islands sample. It will not be further considered here.

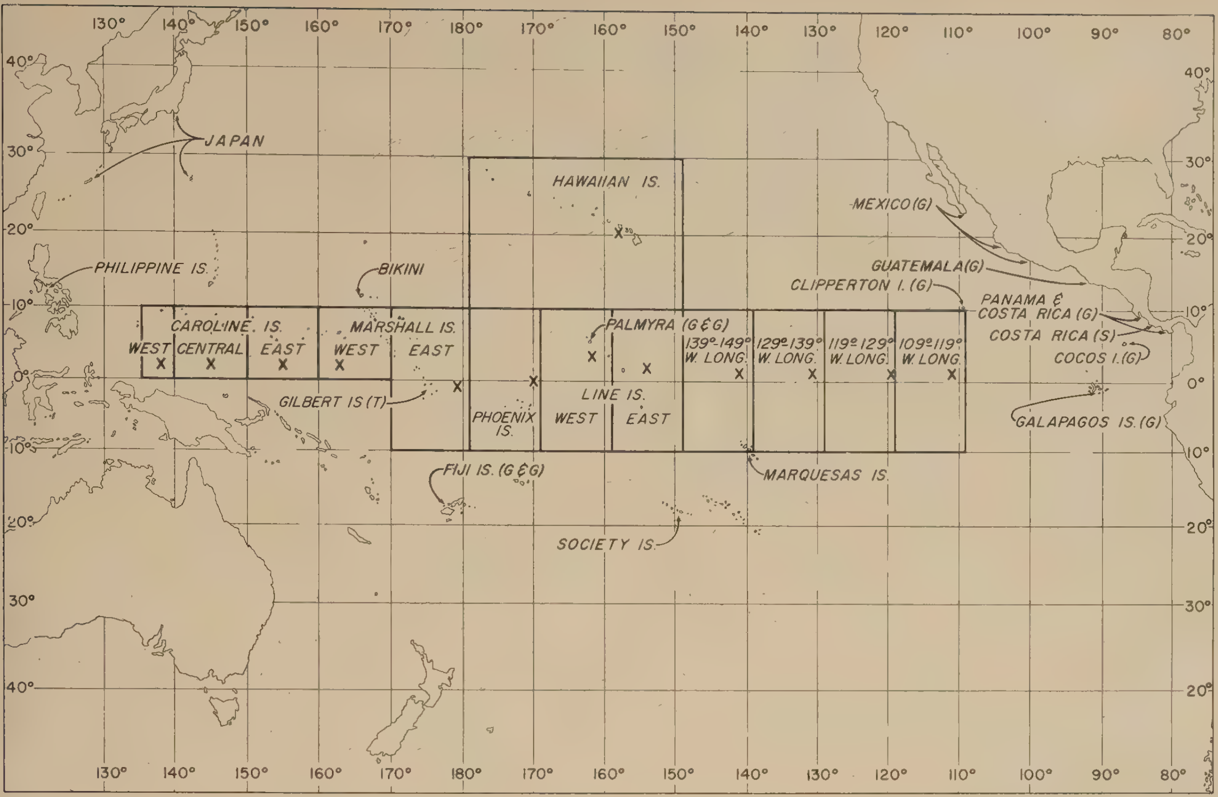
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°
40°
30°
20°
10°
0°
10°
20°
30°
40°
JAPAN
HAWAIIAN IS.
MEXICO (G)
PHILIPPINE IS.
BIKINI
GUATEMALA (G)
CLIPPERTON I. (G)
PANAMA & COSTA RICA (G)
CAROLINE IS.
MARSHALL IS.
PALMYRA (G & G)
WEST
CENTRAL
EAST
WEST
EAST
139°-149° W. LONG.
129°-139° W. LONG.
119°-129° W. LONG.
109°-119° W. LONG.
COSTA RICA (S)
COCOS I. (G)
GILBERT IS (T)
LINE IS.
PHOENIX IS.
WEST
EAST
GALAPAGOS IS. (G)
FIJI IS. (G & G)
MARQUESAS IS.
SOCIETY IS.

FIGURE 2.—Geographic distribution of Pacific samples of yellowfin tuna. (X indicates approximate center of distribution of fish comprising each sample from Hawaii and the equatorial area. (G) indicates Godsil, 1948; (G & G) Godsil and Greenhood, 1951; (S) Schaefer, 1952; (T) Tsuruta, 1954.)

MORPHOLOGICAL CHARACTERS USED

The morphological characters I have used in this study were selected through precedent and experience. The precedent was established by several workers who attempted thorough morphometric studies. None of the recent workers (Schaefer, 1948; Godsil, 1948; or Schaefer and Walford, 1950) explained how they selected their characters, but undoubtedly they were guided by previous research reported in the literature in which yellowfin tuna had been differentiated largely on the basis of fin length. Godsil (1948) defined 16 measurements but presented data on only 6: fork length; head length; and distances from the snout to insertion of first dorsal, second dorsal, anal, and ventral fins. He states that he investigated counts but discarded them because they were unsatisfactory. Schaefer (1948) used five of these measurements (he did not measure snout to insertion of ventral fin). He added the greatest body depth; length or height of the pectoral, second dorsal, and anal fins; longest dorsal finlet and dorsal ray; distance from pectoral fin insertion to insertion of first dorsal fin; length of the base of first dorsal fin; diameter of iris; and length of maxillary. In addition, he obtained four counts: number of dorsal fin rays (including spines if any), dorsal finlets, anal finlets, and gill rakers.

Schaefer and Walford (1950), for part of the specimens measured off Angola, Africa, used the same measurements as Schaefer (1948), but added spread of caudal fin, length of first dorsal spine, least depth of caudal peduncle, greatest width of caudal peduncle at keels, and snout to insertion of ventral fins. They also obtained the same four counts and recorded the sex of some of the fish. Subsequently, this list of measurements was markedly reduced by Schaefer (while he was directing the morphometric program at POFI) to fork length; head length; snout to insertion of first dorsal, second dorsal, anal, and ventral fins; length or height of pectoral, second dorsal, and anal fins; greatest body depth; and diameter of the

TABLE 1.—*Number of tuna measured, by size interval and place of collection*

Area	Number of fish in fork length (cm.) interval of—															Total
	30–39.9	40–49.9	50–59.9	60–69.9	70–79.9	80–89.9	90–99.9	100–109.9	110–119.9	120–129.9	130–139.9	140–149.9	150–159.9	160–169.9	170–179.9	
Mexico [1]	------	------	52	143	155	8	3	------	------	------	------	------	------	------	------	361
Guatemala [1]	------	------	49	54	16	1	------	------	------	------	------	------	------	------	------	120
Panama and Costa Rica [1]	------	1	129	283	282	36	42	43	48	20	3	------	------	------	------	887
Costa Rica [2]	------	------	2	7	3	6	11	6	6	2	------	2	1	------	------	46
Cocos Island [1]	------	6	8	36	128	80	28	2	------	4	10	5	4	------	------	311
Galapagos Island [1]	------	------	97	14	9	65	9	------	------	------	------	------	------	------	------	194
Clipperton Island [1]	------	------	1	21	7	4	2	1	2	------	------	------	------	------	------	38
109°–119° W	------	------	------	------	1	2	------	1	2	3	------	7	5	6	------	27
119°–129° W	------	------	------	------	------	------	------	------	------	3	10	16	14	4	------	47
129°–139° W	------	------	------	1	1	------	1	------	------	5	5	12	10	11	------	46
139°–149° W	------	------	------	------	------	------	------	------	------	4	25	29	33	20	2	113
East Line Islands	------	------	------	1	4	4	8	16	5	12	35	48	52	10	------	195
West Line Islands	------	1	5	16	22	28	22	19	17	11	21	18	7	1	------	188
Palmyra Island [3]	------	------	1	10	24	18	27	10	2	1	------	1	------	------	------	94
Phoenix Islands	------	------	4	19	14	16	19	9	15	15	21	7	2	1	------	142
East Marshall Islands	------	------	------	------	------	------	------	------	2	6	16	16	------	------	------	40
Gilbert Islands [5]	------	------	------	------	------	------	------	------	2	3	13	14	1	------	------	33
West Marshall Islands	2	2	7	1	------	------	------	------	------	------	------	------	4	2	------	18
Bikini Island	------	------	21	6	4	5	4	3	1	------	------	------	------	------	------	44
East Caroline Islands	------	1	18	23	18	19	16	6	14	12	21	9	13	1	------	171
Central Caroline Islands	------	1	6	11	19	21	21	33	27	33	24	13	2	------	------	211
West Caroline Islands	------	------	------	2	1	1	3	------	2	7	1	------	------	------	------	17
Philippines (SW. Panay)	------	1	58	121	62	47	19	9	6	15	11	5	2	------	------	356
Japan	1	11	6	6	7	8	6	1	------	------	------	------	------	------	------	46
Hawaii [2]	------	16	15	3	2	4	9	15	6	17	29	22	15	32	18	203
Hawaii [3]	------	------	42	5	------	11	------	------	1	------	7	11	1	1	------	79
Society Islands	------	2	15	3	2	7	1	------	------	------	------	2	------	------	------	32
Fiji Islands [3]	------	------	1	2	------	3	1	6	------	------	------	------	------	------	------	13
Northeast Africa	------	------	------	5	12	30	------	1	------	------	------	------	------	------	------	48
Angola, Africa [4]	------	1	------	------	11	11	1	------	9	8	9	6	2	2	------	60
Total	3	43	537	793	804	435	253	181	167	181	261	243	168	91	20	4,180

[1] Godsil (1948). [2] Schaefer (1952). [3] Godsil and Greenhood (1951). [4] Schaefer and Walford (1950). [5] Tsuruta (1954).

iris. But another measurement was added—the distance from insertion of the ventral fins to the anterior edge of the vent.

This reduction was undertaken without conclusive evidence that the omitted characters were less satisfactory than those retained; but some reduction was clearly necessary in order to have a manageable number of characters, and we think that the selection was good. The characters retained are, in general, external measurements that differentiate several species of tuna closely related to the yellowfin. Of special importance are length of the pectoral fin, length of the anal and second dorsal fins, and the general body proportions, which are reflected by length of the head and distance to the insertions of several fins. It is reasonable to assume that if these characters have differentiated during evolution of these other tuna species, they may well be differentiating in the evolution of the yellowfin group.

Some characters were excluded because they were troublesome to measure or count. For example, the counting of dorsal and anal finlets is complicated occasionally by the apparent absence of a finlet in the midst of the series. Sometimes it is obvious that a finlet has been torn off, at other times it is uncertain whether there had been a finlet in the space. The diameter of the iris has been omitted because of confusion among our workers between measuring the diameter of the iris and that of the eye. When plotted, these measurements seemed to fall into two groups and we found that measurements had been taken in different ways. We also have not used the gill raker counts, even though we obtained considerable numbers of them, because of uncertainty that our numerous field people were counting gill rakers in the same way. The difficulty is that gill rakers become progressively smaller on one side of the gill arch until covered by skin and, in any gross examination such as must be made in the field, it is always necessary to decide whether certain gill rakers are big enough to be counted. In addition, the number of gill rakers is not entirely independent of length of the fish. In one long series of counts made with great care in the laboratory on yellowfin from a single area, we found a statistically significant association between number of gill rakers and length of the fish.

Thus, the selection of characters has obviously been haphazard and I cannot claim to have selected the best ones. I can say only that they are the principal external characters which have served to differentiate the species of tunas and they

TABLE 2.—*Characteristics of yellowfin tuna morphometric samples*

[Size groups: S, < 80 cm., M, 80–120 cm., and L, > 120 cm.]

Area and size group	Number	Mean fork length (cm.)	Sampling effort				Numbers of fish by gear [1]			Remarks
			Years	Months	Days	Examiners	Longline	Pole and line	Troll	
Mexico: [2] S	361	68.46	2	2	5	1	-----	361	-----	(2)
Guatemala: [2] S	120	62.26	1	1	2	1	-----	120	-----	
Panama and Costa Rica: [2]										
S	887	75.19	3	5	?	1	-----	887	-----	
M										
Costa Rica: [3] M	29	99.88	1	6	?	[4] 2	-----	29	-----	
Cocos Island: [2]										
S	311	82.16	2	2	<6	1	-----	311	-----	
M										
L										
Galapagos Island: [2] S	194	68.32	1	1	?	1	-----	194	-----	
Clipperton Island: [2] S	38	73.89	1	1	3	1	-----	38	-----	
109°–119° W.: L	21	149.82	1	1	5	[4] 2	21	-----	-----	
119°–129° W.: L	47	146.72	1	4	12	4	46	-----	-----	From catches of POFI vessels.
129°–139° W.: L	47	144.67	1	3	15	5	45	-----	2	
139°–149° W.: L	113	148.73	1	3	23	6	109	-----	1	
East Line Islands:										
M	33	102.51	3	8	13	9	17	-----	16	
L	157	145.35	4	9	36	9	149	-----	3	
West Line Islands:										
S	44	68.68	4	9	28	9	1	7	32	
M	87	97.76	4	8	31	9	7	8	63	
L	58	138.13	4	8	23	8	46	1	9	
Palmyra Island: [5]										
S	35	72.49	1	1	Ca. 12	1	-----	-----	-----	All fishing done close to Palmyra, Fanning and Christmas Islands.
M	57	94.38	1	1		1	-----	-----	-----	
Phoenix Islands:										
S	37	67.67	3	5	16	5	1	9	27	From catches of POFI vessels.
M	59	98.23	2	6	24	7	-----	16	42	
L	46	133.53	3	6	26	7	19	13	9	
East Marshall Islands: L	40	136.34	1	1	8	3	32	-----	-----	
Bikini Island: S	31	59.03	1	2	?	1	-----	-----	31	Measured by J. C. Marr.
East Caroline Islands:										
S	60	65.27	2	6	24	[4] 3	59	1	-----	Obtained by POFI observers on Japanese mothership expeditions.
M	55	98.26	2	4	20	[4] 2	55	-----	-----	
L	56	139.95	2	5	21	[4] 3	56	-----	-----	
Central Caroline Islands:										
S	37	67.94	1	3	17	[4] 2	36	1	-----	
M	102	100.88	1	3	22	[4] 2	102	-----	-----	
L	72	132.29	2	4	17	[4] 3	72	-----	-----	
Philippines:										
S	242	65.19	-----	-----	-----	-----	-----	-----	-----	Contributed by D. V. Villadolid, Philippine Bureau of Fisheries.
M	81	90.74	-----	-----	-----	-----	-----	-----	-----	
L	33	132.99	-----	-----	-----	-----	-----	-----	-----	
Japan: S	31	57.73	1	2	7	1	1	28	-----	Measured by POFI observers in Japan.
Hawaii:										
S	36	52.35	2	7	17	4	-----	19	5	From POFI catches and Honolulu fish market.
M	34	101.95	1	7	21	[4] 4	15	15	2	
L	133	150.04	1	7	77	[4] 4	129	1	-----	
Hawaii: [5]										
S	47	57.01	1	-----	-----	1	-----	-----	-----	From near Johnston Island and near islands northwest of Kauai.
L	20	142.96	1	-----	-----	1	-----	-----	-----	From Honolulu market.
Society Islands: S	22	57.30	1	-----	-----	4	-----	22	-----	From frozen fish landed in Honolulu.
Northeast Africa: S	48	79.15	1	2	9	1	-----	-----	-----	Courtesy of FAO, measured by A. Fraser-Brunner.
Angola, Africa: [6]										
M	21	97.64	1	1	4	1	-----	-----	-----	
L	27	137.67	1	1	4	1	-----	-----	-----	

[1] A few specimens lacked record of gear used. [2] Statistics based on curvilinear regressions, Godsil (1948). Additional information from correspondence. [3] Schaefer (1952). [4] More than half of samples measured by one person. [5] Godsil and Greenhood (1951). [6] Schaefer and Walford (1950).

appear to be the most variable ones within the yellowfin group that can be measured with precision and consistency by different people.

METHODS OF MEASUREMENT

Our methods of measuring tuna follow the specifications given by Marr and Schaefer (1949). I think we have measured the fish exactly as they intended, but we slightly modified their definitions to overcome some confusion existing among our measurers. The most recent instructions given POFI workers have been as follows:

The measurements described are all made in millimeters with calipers or dividers, depending on the size of the fish and the distance to be measured. All distances are straight lines. The tip of the fixed arm of the calipers (or one point of the dividers) is applied to the first point mentioned and the tip of the sliding arm of the calipers (or the other point of the dividers) is applied to the second point mentioned. Where a choice of sides is involved, all measurements and counts are made on the left side of the fish. Fin insertions are to be determined while holding the fin approximately perpendicular to the contour of the fish.

Fork length.—(Total length of Marr, Schaefer, and Godsil.) The distance from the tip of the snout (most anterior point on upper jaw), with jaws closed, to the cartilaginous median part of the caudal fork (seating the sliding arm of the caliper firmly and thus depressing the small fleshy flap extending posteriorly).

Head length.—Distance from the tip of the snout to the most posterior point on the margin of the subopercle (depressing the fleshy flap extending posteriorly).

Snout to insertion of first dorsal fin.—The distance from the tip of the snout to the insertion of the first dorsal. The insertion of the first dorsal is the intersection of the anterior margin of the first dorsal spine, when the fin is held erect, with the contour of the back. This point is identical with the most anterior point of the first dorsal fin slot.

Snout to insertion of second dorsal fin.—The distance from the tip of the snout to insertion of the second dorsal. The insertion of the second dorsal is not so clearly defined as the insertion of the first dorsal, particularly on larger fish; but it is the intersection of the anterior margin of the second dorsal with the contour of the back when the fin is held erect. When the second dorsal is raised, the determined point should be marked with thumbnail or scalpel.

Snout to insertion of anal fin.—The distance from the tip of the snout to the insertion of the anal fin. The insertion of the anal fin is determined in the same manner as the insertion of the second dorsal.

Snout to insertion of ventral fin.—The distance from the tip of the snout to the insertion of the ventral. The insertion of the ventral is the intersection of the anterior margin of the ventral, when the fin is extended, with the contour of the body.

Insertion of ventral fins to anterior edge of vent.—The midline distance from the insertion of the ventrals to the anterior edge of the vent.

Greatest body depth.—The greatest distance between the dorsal and ventral contours perpendicular to the axis of the fish. The measurement is taken from the dorsal body contour to the ventral body contour, with the first dorsal fin depressed in its slot. It is oriented by reference to the dorsal spine, the insertion of which is at or nearest to the upper end of the vertical. Dorsal spines are counted posteriorly, the most anterior spine being the first.

Length of pectoral fin.—The distance from the anterior end of the fin slot to the most posterior point, taken with the pectoral fin extended posteriorly and opposed to the side.

Height (length) of second dorsal fin.—The distance from the insertion of the second dorsal fin to its distal end, with the fin in a normal position. Note that this fin is often extended in a long filament, especially in large Neothunnus, and care should be taken to notice if this extension is frayed.

Height (length) of anal fin.—The distance from the insertion of the anal fin to its distal end, with the fin in a normal position. Remarks under height of second dorsal fin apply here.

Diameter of iris.—The greatest diameter measured to the margin of the yellow iris and the adjoining black tissue. This is generally not a line parallel to the median line of the body.

Number of gill rakers.—The number of anterior rakers on the most anterior gill arch on the left side of the fish (some species also have posterior rakers on this same arch). The counts of the rakers on the two arms of the arch are kept separate. For example, 10+20=30 gill rakers with 10 on the upper arm and 20 on the lower. The counts include all rakers that project above the surrounding epithelium. We have encountered no difficulty in assigning rakers near the angle of the arch to one arm or the other.

Sex.—Determined by inspection. Very immature males and females may be difficult to distinguish. Ovaries, which are tubular, may often roll between the fingers, while testes, which are solid, will turn over. The testes of ripening or ripe males are enlarged, solid, white bodies, not round in cross section. The ovaries of ripening or ripe females are enlarged, turgid, pink or yellow-orange bodies, round in cross section. Ova may often be distinguishable with the naked eye. The testes of spawned-out males are less turgid, tougher, and pinker than those not spawned, and are difficult or impossible to distinguish from maturing testes in early stages. The ovaries of spawned-out females are hollow, more or less flabby, saclike tubes.

Weight.—Should be determined in pounds on steelyards of proper range. Do not weigh on steelyard having capacity greater than about three times the weight. Be sure to subtract the weight of any hooks used to hold the fish. Record weight to smallest unit on steelyard. Note if fish is weighed in pieces.

IMPORTANT

Check steelyards before each cruise. Errors must not exceed 1 percent.

Check calipers each time they are used. Errors must not exceed 1 mm.

In addition to these instructions, diagrams were provided on the back of each field sheet (fig. 3).

All measurements of distances exceeding about 55 mm. have been obtained with sliding calipers. This lower limit occurs because some of our calipers will not measure closer than that and hence the shorter distances have been measured with dividers and millimeter rule. All measurements are the actual distance between two points and not the distance parallel to the midline of the body and between perpendiculars as specified by LeGall (1951) for body measurements of European tunas.

Our calipers have usually been of two sizes, 1 m. and 2 m. They evolved through brass and aluminum to standard wooden meter sticks.

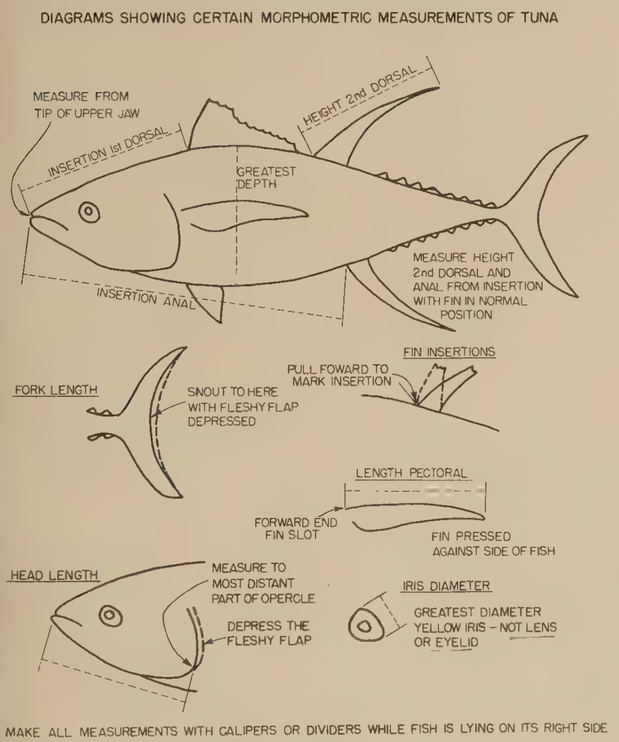
DIAGRAMS SHOWING CERTAIN MORPHOMETRIC MEASUREMENTS OF TUNA
MEASURE FROM TIP OF UPPER JAW
INSERTION 1st DORSAL
HEIGHT 2nd DORSAL
GREATEST DEPTH
INSERTION ANAL
MEASURE HEIGHT 2nd DORSAL AND ANAL FROM INSERTION WITH FIN IN NORMAL POSITION
FORK LENGTH
SNOUT TO HERE WITH FLESHY FLAP DEPRESSED
FIN INSERTIONS
PULL FOWARD TO MARK INSERTION
LENGTH PECTORAL
FORWARD END FIN SLOT
FIN PRESSED AGAINST SIDE OF FISH
HEAD LENGTH
MEASURE TO MOST DISTANT PART OF OPERCLE
DEPRESS THE FLESHY FLAP
IRIS DIAMETER
GREATEST DIAMETER YELLOW IRIS – NOT LENS OR EYELID
MAKE ALL MEASUREMENTS WITH CALIPERS OR DIVIDERS WHILE FISH IS LYING ON ITS RIGHT SIDE

Figure 3.—Diagrams on the back of the field data sheet showing certain morphometric measurements of tuna.

The 1-m. caliper consisted simply of a fixed jaw and a slider on a standard meter stick. If the meter sticks are selected with care to get straight ones, we find it easy to maintain the accuracy within 1 mm. by checking the caliper prior to each use. (We found this checking equally essential with the metal calipers because of the ease with which they can be bent.) For the 2-m. calipers we put two meter sticks end to end in a sheet aluminum channel. The channel was made slightly longer than the two meter sticks to permit a third meter stick with a movable jaw to be inserted when we were measuring large sharks or marlins more than 2 m. long.

Almost all of our measurements were obtained in the field and usually on shipboard. In equatorial areas on POFI vessels it was customary to measure up to about 10 tuna of all species during the course of a day's fishing. During longline fishing operations, which were usually carried out along a line of stations, this ensured that the sample included tunas from a wide-spread area. On the Japanese mothership expeditions in the Caroline Islands area, POFI observers measured fish on the deck of the mothership a few days after capture by catcher vessels.

The original measurements not obtained on POFI vessels came from a variety of sources. In the Honolulu area most measurements were from specimens received at the fresh fish market. The Japanese specimens were measured by members of the POFI reconnaissance team that visited Japanese markets in 1949. Specimens from the Society Islands were measured from the catch of the vessel *Hawaiian Tuna* when they were landed at the Honolulu market and after they had thawed.

METHODS OF COMPUTATION

As indicated in the general discussion on the comparison of morphometric data, I have not considered ratios or indexes but have used regression analysis entirely in order to control the effect of size of fish in our comparisons. I have used the regressions for yellowfin tuna proposed by Schaefer (1948), who stated that the original measurements provided a satisfactory straight-line relation with fork length in the case of head length, snout to insertion of first dorsal fin, snout to insertion of second dorsal fin, snout to insertion of anal fin, and greatest body depth.[4] For the length of the pectoral fin he used the actual length of the fin with the logarithm of fork length, and for heights of the second dorsal and anal fins he used the logarithm of length of fin with the logarithm of fork length. For the other character, the distance from the insertion of the ventral fins to the anterior edge of the vent, which Schaefer (1948) did not use, no transformation is needed to obtain a reasonably straight line.

After accumulating several thousand sets of measurements for several species of tunas, we found that the labor of analysis was beyond our facilities and we turned to the International Business Machines Corporation for assistance. On most of our material, in which the original field data sheets had one fish per sheet, codes were added for species, locality, 10-cm.-length group, month, year, sex, and the examiner. Certain measurements were transformed to logarithms and the code and measurements were punched on cards. It was then possible to square, cross multiply, and tabulate automatically. A complete tabulation of sums, sums of squares, and sums of the products for regression analysis was obtained, arranged according to species, locality, and 10-cm.-length group. Subsequently, special tabulations of the material were made as needed.

After the data had been completely tabulated and totaled, scatter diagrams were made for each character on all specimens from each area to permit an immediate judgment of aberrant observations. If any data were obviously aberrant,[5] they were checked with the original field data, and, if plotted as recorded, they were assumed to be in error and were discarded. The regression line was then computed and plotted along with parallel lines plus and minus three standard deviations from regression. At this time, any remaining points more than three standard deviations from regression were assumed to be in error and were dropped. Then, final regression and the standard deviation from regression were computed. I have not tabulated the number of discarded observations, but I estimate it to be less than 2 percent of the total.

Discarding any data is questionable because correct but unusual observations may be discarded. By my method, however, most of those dropped were far removed from the line. The rejected values frequently were so located that one suspected that digits had been transposed or errors made in the decimeter digit. I believe that few if any correct observations were discarded. Furthermore, some culling is desirable for all data of this kind which have been collected under difficult field conditions where it is not practical to check original measurements.

Checks were made at all stages of computations. All IBM card punching was verified. All desk calculator operations that could not be independently checked were repeated. Finally, the plots of the regression line and standard deviations from regression provided a visual check which detected any but trivial errors.

SELECTION OF REGRESSION EQUATIONS

In the analysis of yellowfin tuna morphometrics, two fundamental statistics, mean and variance, are required. Both must be unbiased estimates of corresponding population parameters. These statistics are estimated from the best regression formulae. If I apply straight line regressions to data that are curvilinear, then my estimates of the means may diverge an unknown amount from the population parameter and the estimates of variance will tend to be excessive. On the other hand, curvilinear regression techniques tremendously increase already laborious calculations and for practical reasons should be avoided unless fully justified.

The two authors who have dealt with relative growth of the yellowfin tuna are in fundamental disagreement on whether curvilinear regression is needed for several characters. Schaefer (1948: 117) stated, "Over the range of sizes considered, all the characters measured, with the exception of the lengths of the pectoral, second dorsal and anal fins, bear a linear relationship to the length of the fish." For the length of the pectoral fin he used the logarithm of fork length and for the other two fin dimensions he used the logarithm of both fin length and fork length and simply states, without offering proof, that these transformations are appropriate. Schaefer later (1952) cautioned that the relationships were only approximations that did not completely describe the relation between fork length and size of the body part. On the other hand, Godsil (1948: 7) stated—

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[4] An evaluation of the regression formulae will be found in the following section.

[5] This was usually more than about 15 percent (about four standard deviations) of the size of the character away from the general trend.

> Plotting to a large scale the actual measurements of a given character against body length in each case, revealed that the sample regressions were nearly but not quite linear. Of the various functions tried, the expression $Y=a+bx+c\frac{1}{x}$ (where x=body length in each case and Y=the dependent variable) resulted in the best fit.

The other functions tried included $y=a+bx$, $y=a+bx+cx^2$, $y=a+bx+cx^2+dx^3$, $y=ax^b$, and $y=ae.^{bx}$ He also stated that the reduction in the sum of the squared deviations from the above expression when compared with the sum from the linear regression was in most cases highly significant. He offered no statistical data supporting this assertion; but his graphs, with the plotted points and curved lines, show clearly that the data for head length and snout to the insertions of first dorsal, ventral, second dorsal, and anal fins are slightly curvilinear and the computed lines fit well. The curvilinearity in Godsil's data is further puzzling because Schaefer and Walford (1950) presented data for characters used by Godsil that show no curvilinearity.

Therefore, it is desirable to examine in greater detail the source of curvilinearity in Godsil's data. This may be done by comparing the mean-square deviations from linear regression with those from curvilinear regression (table 3). When such comparisons are summed for the 13 samples for each character, I find that curved lines significantly reduced the mean square of pooled data as well as the mean square of within-sample data for each character. I notice, however, that for all characters reduction in the mean square from linear to curvilinear regression is much greater for pooled data than it is for within-sample data. Such differences between pooled and within-sample data suggest than a major part of the curvilinearity is between samples rather than within samples.

More conclusive evidence of the source of curvilinearity is to be found by examining the significance of the reduction in the mean square, character by character and sample by sample (table 3). Here significant or highly significant curvilinearity for most characters occurs in samples 1, 3, 4, 5, 6, and 7. In the remaining seven samples, 2 and 8 through 13, only four instances of a significant but not highly significant reduction in mean square occur in 35 comparisons. Since two significant reductions would be expected to occur by chance in this number of comparisons, little importance can be attached to the four. Clearly, curvilinearity is associated with certain samples and not with certain characters for all samples, as would be expected from a truly curvilinear regression of body part on fork length.

One characteristic of the samples that might be associated with curvilinearity is size, since it is obvious that very large samples (DF=385, 348) show curvilinearity whereas small samples (DF=25, 36, 67) do not. Among the eight samples of intermediate size, however, four, with degrees of freedom equaling 192, 121, 98, and 96, show no more than one character with significant curvilin-

TABLE 3.—*Mean-square deviations from linear and curvilinear regressions of yellowfin morphometric measurements*

[Measurements from Godsil, 1948]

Sample number	Degrees of freedom [1]	Length of head		Snout to insertion of—								Date of collection [2]
				First dorsal fin		Second dorsal fin		Anal fin		Ventral fin		
		Linear	Curvilinear	Linear	Curvilinear	Linear	Curvilinear	Linear	Curvilinear	Linear	Curvilinear	
1	92	7. 84	**6. 69	14. 53	**13. 49	20. 15	*19. 22	20. 26	**17. 66	13. 07	**11. 41	Mar. 13, 1939.
2	96	5. 71	5. 68	10. 06	10. 21	12. 83	12. 45	19. 59	*18. 47	11. 89	11. 79	Mar. 8, 1939.
3	166	10. 80	*10. 58	12. 40	12. 10	21. 17	**19. 29	26. 93	*26. 44	16. 87	17. 10	Apr. 25, 27, 1940.
4	385	11. 06	**10. 34	20. 98	**19. 70	32. 46	**29. 91	29. 40	30. 63	25. 07	**24. 70	Nov. 5 to Dec. 7, 1936.
5	348	11. 08	**8. 91	18. 97	**15. 72	22. 95	**15. 59	22. 63	**19. 70	20. 06	**19. 07	Jan. 14 to Feb. 13, 1937.
6	118	5. 82	**5. 32	10. 66	**9. 24	13. 27	13. 21	13. 40	13. 44	12. 86	*12. 32	Mar. 26, 27, 1939.
7	141	18. 40	**14. 19	25. 57	**22. 22	38. 00	**32. 30	34. 09	**30. 69	31. 75	**28. 29	Jan. 16 to 19, 1937.
8	192	7. 73	8. 37	12. 01	12. 49	11. 62	12. 55	16. 56	16. 85	14. 07	15. 71	Apr. 1 to 19, 1940.
9	67	6. 37	6. 29	4. 84	14. 55	12. 81	13. 06	16. 07	16. 15	8. 42	8. 58	May 12, 1940.
10	121	5. 45	*5. 26	9. 91	10. 30	11. 19	11. 03	15. 74	16. 43	13. 79	14. 16	Jan. 21 to Feb. 10, 1937.
11	36	7. 81	7. 83	9. 94	*8. 83	21. 92	21. 03	13. 97	14. 17	18. 63	19. 32	Mar. 22 to 24, 1940.
12	25	6. 92	7. 21	7. 84	8. 17	15. 16	15. 75	23. 60	24. 54	21. 12	21. 96	Apr. 29, 1940.
13	98	8. 28	8. 32	14. 99	15. 11	13. 04	*12. 66	16. 72	16. 84	14. 27	14. 28	Mar. 30, 31, 1940.
Pooled-sample variance	1909	12. 07	**9. 53	19. 07	**15. 78	24. 93	**20. 40	27. 25	**25. 85	19. 91	**19. 31	
Within-sample variance	1885	9. 71	**8. 80	16. 14	**14. 94	21. 69	**19. 24	22. 65	**21. 99	18. 73	**18. 34	

[1] Varies slightly with different characters. [2] Supplied by Godsil in personal communication. * Statistically significant reduction in mean square ($0.05 > p > 0.01$). **Highly significant reduction in mean square ($p < 0.01$).

earity. The other four samples of intermediate size show highly significant curvilinearity in at least one character and significant curvilinearity in more than half of the characters. It is likely that something other than sample size alone has caused curvilinearity.

Another source of curvilinearity may be accidents of sampling. Such accidents appear to be rather likely because most of Godsil's samples (table 2) were obtained on a single day or over a period of a few days. It is well-known that yellowfin school by size, and when one of the larger samples includes a considerable range in sizes it is probable that it was obtained from only a few schools of different average size. If the sample included schools of slightly different morphological characteristics and also of different mean size, there would be two sources of regression—one within schools fished and the other between schools fished. The combined regressions might appear to be curvilinear.

Therefore, when I examined our data for curvilinear regression I turned first to the sample that I considered had the best coverage of the area sampled and that contained a good size distribution of fish. It was the sample from the western Line Islands area, obtained during 13 different months with the majority of the fish caught by longlining and trolling and measured by 12 different measurers. During both longlining and trolling operations, it was customary to measure only a few fish a day (rarely more than 10), and thus these fish came from several dozen different schools and as many different locations within the area. There are 188 sets of measurements available in this sample, with good numbers in most 10-cm. length groups from 50 to 160 cm.

Evidence of curvilinearity was sought in the plots of complete data that were made to check each sample. Some evidence of curvilinearity appeared in the plots for certain characters, but the scatter of points around the line made interpretation difficult. Hence, I sought a way to magnify any curvilinearity and plotted the deviations of the 10-cm. group means from the rectilinear regression equations for each character in the sample (fig. 4). These equations were based on the transformations, proposed by Schaefer (1952), which are log fork length and log height of second dorsal fin, log fork length and log height of anal fin, and log fork length and length of pectoral fin. The data for all other characters were not transformed.

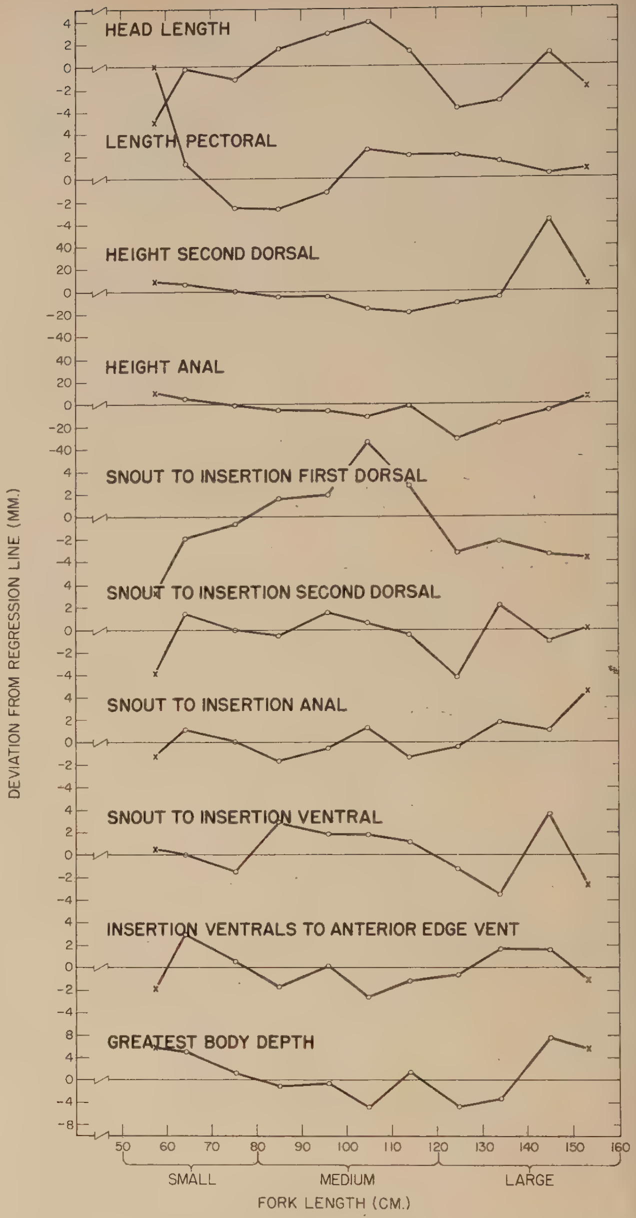

FIGURE 4.—Sample of yellowfin tuna from western Line Islands area. Deviations of 10-cm. group means from regressions were used. (X, average of less than 10 fish; 0, average of 10 or more fish.)

The graph suggests that some curvilinearity occurs in several characters. If a random distribution of 10-cm.-group means about the regression line is assumed, a line connecting the group means would be expected to cross the regression line an average of five times (with 11 points). To the contrary, for four characters—

length of pectoral, height of second dorsal fin, height of anal fin, and snout to insertion of first dorsal fin—the lines crossed only twice. In the case of only one character—the snout to insertion of second dorsal fin—did the lines cross more than the most probable number of times.

The question then arose whether the curvilinearity prevailed in other samples, and I made a similar analysis of our other two large samples that also are well distributed over a wide range of lengths. They were the samples from the eastern Caroline Islands and the central Caroline Islands, which contained 171 and 211 sets of measurements, respectively. Similar plots of deviations of 10-cm.-group means from the rectilinear regression lines (figs. 5 and 6) indicated

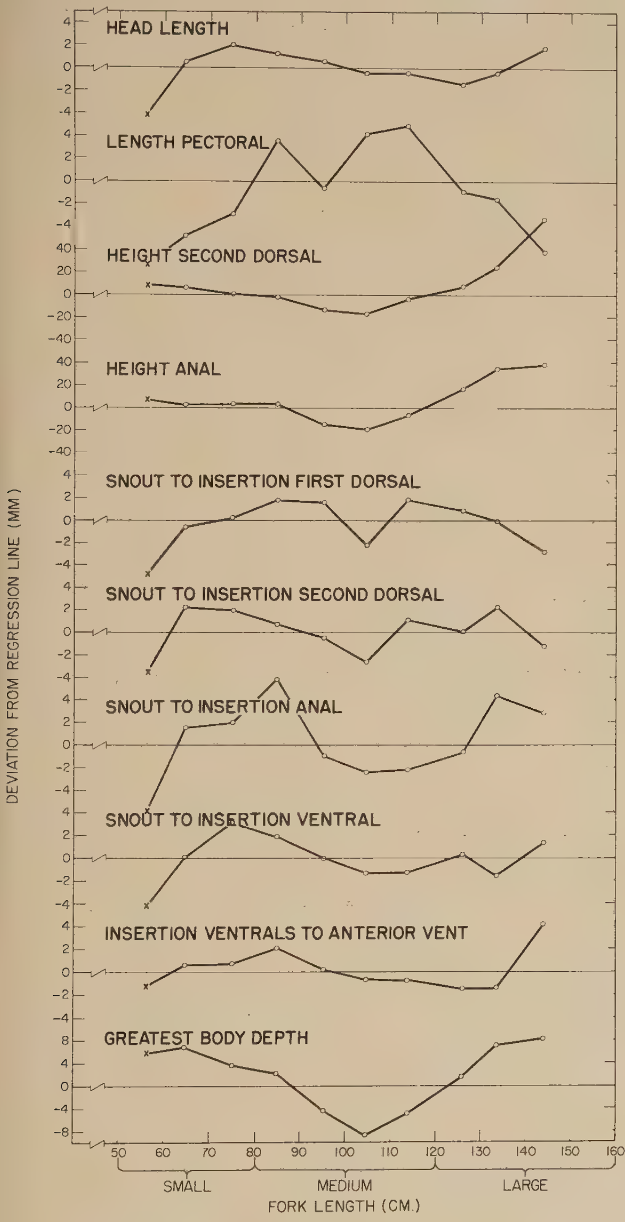

FIGURE 5.—Sample of yellowfin tuna from central Caroline Islands area. Deviations of 10-cm.-group means from regression. (X, average of less than 10 fish; 0, average of 10 or more fish.)

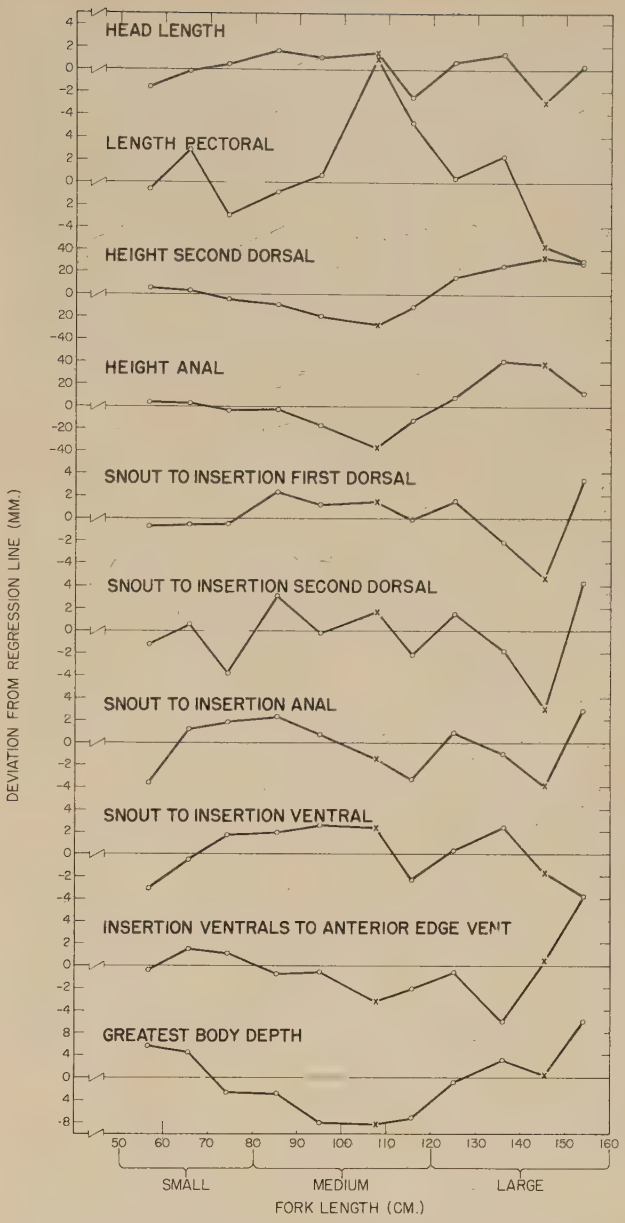

FIGURE 6.—Sample of yellowfin tuna from eastern Caroline Islands area. Deviations of 10-cm.-group means from regression. (X, average of less than 10 fish; 0, average of 10 or more fish.)

again that the lines cross less than the expected number of times for most characters.

When compared, the deviations from regressions of all three areas indicate that they tend to form a curve concave upwards for height of second dorsal fin, height of anal fin, and greatest body depth. Other characters, especially head length, snout to insertion of first dorsal fin, and snout to insertion of ventral fin, appear sinuous with some tendency for the line connecting means to start below the regression, then go above, then below, and then upward again. The line appears to be curved for length of the pectoral fin, but in a different way in each sample.

I conclude that for most characters in these large samples some curvilinearity remains that is not associated with sampling, but is rather an expression of the allometric growth of the fish. Furthermore, it is an irregular allometry which is not readily expressed by any linear or simple curvilinear formulation.

Such curvilinearity would not be troublesome if all samples had similarly distributed lengths, in which case it would probably be satisfactory to use the regression techniques proposed by Schaefer (1948). The rather small amount of curvilinearity would result in some bias in mean, variance, and regression constants, but if such bias were similar among samples it would not matter. However, it has not been possible to obtain samples covering a uniform range of lengths. In numerous areas, particularly along the Pacific Equator, where we have fished only with longline gear, we have obtained only very large fish, and in other areas, where fishing has been done only by trolling, we took mostly small fish.

The compromise solution has been to split the samples into three size groups and compare them at three different standard lengths, each very close to the grand mean of its size group. The following groups have been used:

Small (S)—fish less than 80 cm., most of which are more than 50 cm. and which have been compared at a length of 65 cm. (about 12 lb.); medium (M)—fish from 80 to 120 cm., compared at a length of 100 cm. (about 43 lb.); large (L)—fish more than 120 cm., most of which are less than 170 cm. and which have been compared at a length of 140 cm. (about 118 lb.).

Further restrictions were adopted: first, to avoid uncertainties due to the small samples it was required that there be more than 20 specimens in each size group, and second, to minimize the effect of any curvilinearity remaining within a size group, it was required that more than 10 percent of the sample be above and more than 10 percent below the comparison size. For example, in Godsil's sample from Panama and Costa Rica there were 23 fish between 120 and 140 cm. and none above 140 cm. This part of his sample was not considered in the large group, whereas his sample from Cocos Island including 23 fish ranging from 120 to 160 cm., with 9 above 140 cm., was considered. One sample remains that is not well distributed in fork length—the one from northeast Africa. It has been used, but the comparisons are made with reservations.

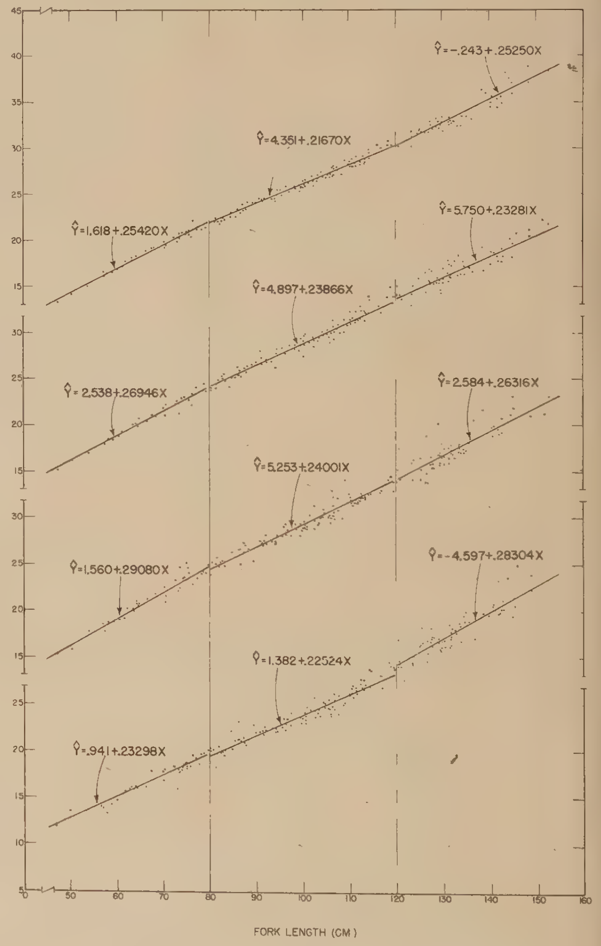

Figure 7A.—Regressions of head length, distances from snout to insertions of first dorsal and ventral fins, and greatest body depth in yellowfin tuna from central Caroline Islands area.

The fit of the lines to the three size groups may be judged from the plots of the data from the central Carolines area (figs. 7A, 7B, and 7C). Each of the three separate lines appears to be a good fit in its limited range, but when projected beyond the range it may rapidly diverge from the plotted points. The tendency that has been noted toward a sinuous line in certain characters is again evidenced in the plots and in the changing regression constants. I judge, however, that any remaining curvilinearity within each size group is much less than the dispersion of points about the line and that samples within each size group may be compared with little fear of erratic results due to curvilinear regression.

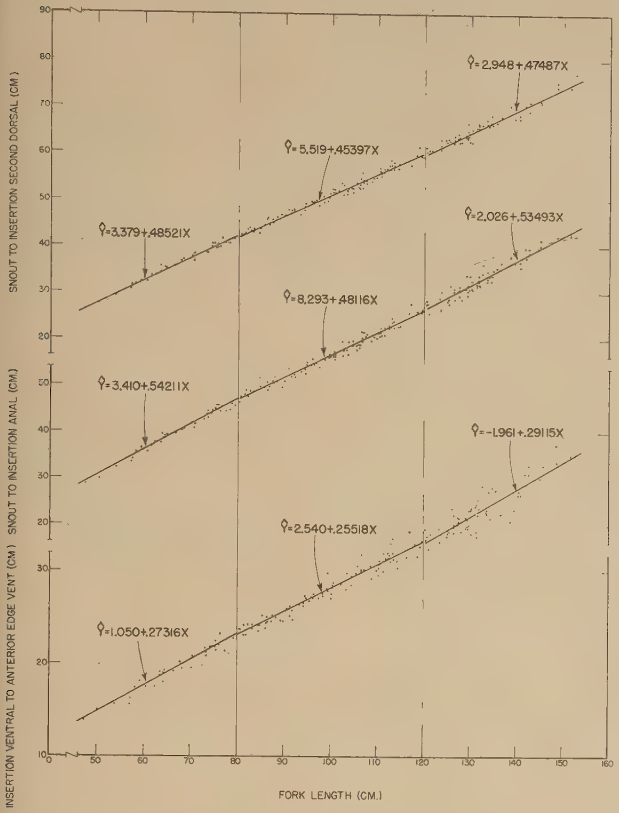

Figure 7B.—Regressions of distances from snout to insertion of second dorsal and anal fins and distance from insertion of ventral fin to anterior edge of vent, in yellowfin tuna from central Caroline Islands area.

RELIABILITY OF SAMPLE STATISTICS

In addition to determining methods of regression analysis that will give reliable estimates of mean and variance the reliability of the raw data must be assessed. Two matters may be examined: first, the adequacy of the sampling, and second, the accuracy of the measurements.

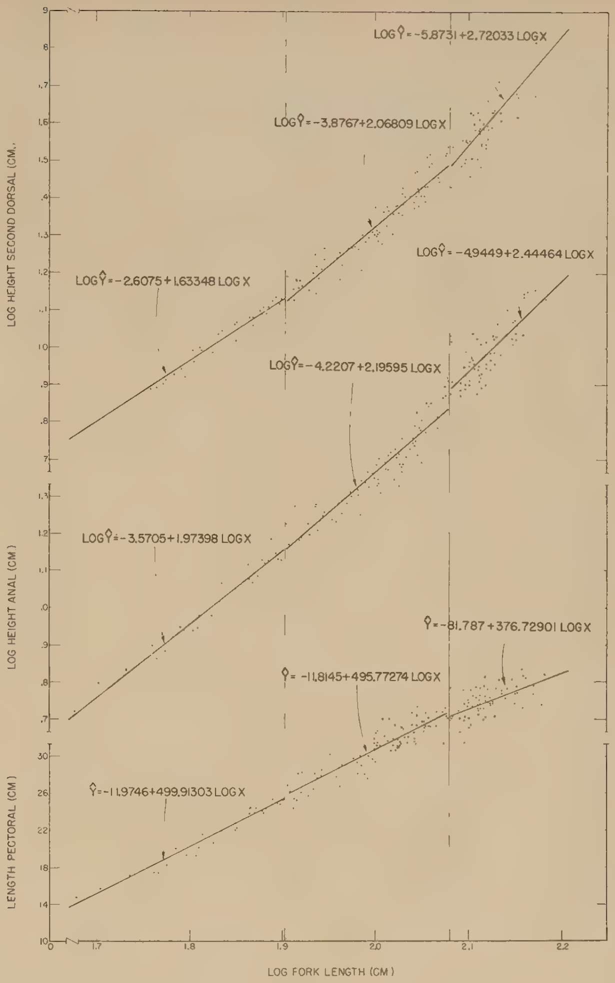

Figure 7C.—Regressions of log heights of second dorsal and anal fins and length of pectoral fin, in yellowfin tuna from central Caroline Islands area.

An ideal sample of yellowfin tuna for a morphometric study would be representative of all sizes of tuna in the specified area during the period of study. Such a sample would contain a distribution of sizes proportionate to the numbers of each size in the ocean and would be randomized over the time and area covered. This ideal is far out of reach because it is not possible to catch all of the sizes, as each fishing gear selects certain size groups, and it has not been possible to fish any area at randomly selected locations or times.

Consideration of the habits of the yellowfin suggests, however, that satisfactory samples may be obtained from a relatively limited coverage.

The yellowfin is a schooling species (Murphy and Elliott, 1954), and I have suggested that schools in a limited area may vary slightly in their morphometric characteristics (p. 406). The yellowfin are fast swimmers, however, and it seems probable that they could cover hundreds of miles in a few days. Furthermore, the larger yellowfin at least are entirely independent of coastal regions. The ocean in which they are found is relatively uniform, with no absolute barriers to migration, although the yellowfin do prefer certain areas, presumably where they find the most food. So it is possible that a sample made up of subsamples from numerous, different schools may be adequately representative of an area even though the area is not randomly covered. The schools may be assumed to have been randomly swimming in the area. A similar assumption with regard to time is less safe because many species migrate annually, and even if yellowfin are present in an area throughout the year, they might be different spawning groups.

Even though the ideal sample cannot be obtained, samples with widely varying coverage in area and time (table 2) may be compared. As the samples were extended in space and time, however, they were taken by an increasing number of people, who may have varied in their techniques of measurement. Therefore, the problems of sampling and precision in measuring the fish must be considered simultaneously, and here I digress briefly to consider the problem of obtaining consistent measurements of yellowfin.

Fortunately, all tunas are easy to measure consistently. The body is stiff, and even when not in rigor mortis has almost no tendency to bend when the fish is laid on a flat deck on its side. The parts to be measured were accurately defined by Marr and Schaefer (1949). The numerous measurers from POFI have compared their methods—almost no one measured tuna without first working with someone who had measured them before—and most differing interpretations of the definitions have been quickly settled. Nevertheless, I consider that minor differences of technique must have occurred both among POFI and other measurers, and the problem is to assess how great the differences have been.

One approach to this problem might be to have different people repeat measurements on the same fish and then analyze the differences. We have made repeat measurements to standardize our methods but have not analyzed the differences, because our concern is with what people have done independently and routinely and not what they could do under experimental conditions.

It will not be possible to separate the differences in technique from differences of time and area, but the combined problem can be approached by examining the variance in relation to coverage of the sample and number of measurers. Also mean values and overlap of closely related samples obtained by different measurers can be compared. The latter comparison must be left until I have introduced the method of comparing means and overlap.

The variance itself is not suitable for our comparison. Better is the standard deviation from regression $S_{y.x}$, which is directly indicative of the spread of points about the line, but it obviously is related to the size of the character, even when the characters have been transformed to logarithms. So I have used a kind of coefficient of variation,

$$C=\frac{100\ S_{y.x}}{\bar{x}},$$

to eliminate the effect of size of character $\bar{x}$ and so obtain a better mean value for all characters in a sample.

These coefficients of variation have been computed for each character in each sample and are shown in table 4 (except the samples of Godsil (1948) from Panama and Costa Rica and from Cocos Island, in which his curvilinear regressions were used and in which the range spreads extensively over two or more of our size groups).

Several samples contained measurements for only five characters, and hence the sample means and the grand means were computed from these five characters only.

This table shows close agreement among grand means of the coefficients of size groups for the five characters, which indicates that the standard deviation from regression is almost exactly related to size of the fish. Further, there is some difference among characters: length of pectoral fin and greatest body depth have a high coefficient; log heights of second dorsal and anal fins show coefficients that increase with size of fish; distances from snout to insertion of second dorsal and anal fins have the lowest values.

TABLE 4.—*Coefficients of variation of yellowfin morphometrics*

Area and size[1]	Length of head (1)	Length of pectoral fin (2)	Weight of second dorsal fin (3)	Weight of anal fin (4)	Snout to insertion of—				Greatest body depth (9)	Insertion ventral to anterior edge vent (10)	Means[2]
					First dorsal fin (5)	Second dorsal fin (6)	Anal fin (7)	Ventral fin (8)			
Mexico:[3] S	1.38	---	---	---	1.70	1.05	1.04	1.60	---	---	1.35
Guatemala:[3] S	1.32	---	---	---	1.64	1.06	.96	1.76	---	---	1.35
Costa Rica:[4] M	1.75	3.13	1.67	1.85	1.76	1.38	.95	---	3.14	---	1.46
Galapagos Island:[3] S	1.42	---	---	---	1.61	.92	.99	1.71	---	---	1.33
Clipperton Island:[3] S	1.33	---	---	---	1.36	1.18	.85	1.83	---	---	1.31
109°–119° W.: L	1.94	3.58	1.32	2.55	3.03	1.44	1.10	2.35	2.19	2.88	1.97
119°–129° W.: L	2.20	4.68	2.58	2.53	2.01	1.18	1.38	2.90	4.29	2.80	1.93
129°–139° W.: L	1.16	4.17	2.66	2.58	2.07	1.33	1.24	2.04	4.09	2.61	1.73
139°–149° W.: L	1.81	3.50	2.47	2.60	2.23	1.28	1.33	2.14	2.96	2.72	1.76
East Line Islands:											
M	1.57	3.03	2.50	2.34	2.02	1.34	1.63	1.84	3.24	2.27	1.68
L	1.82	4.05	2.57	2.71	2.44	1.62	1.33	2.55	2.51	2.54	1.95
West Line Islands:											
S	2.28	3.77	1.56	1.55	2.63	1.34	1.63	2.53	3.43	2.65	2.08
M	2.16	4.40	2.15	2.84	2.27	1.48	1.55	2.70	4.19	2.23	2.03
L	1.96	2.88	2.44	2.26	1.76	1.29	1.11	1.94	3.19	2.64	1.61
Palmyra Island:[5]											
S	2.02	---	---	---	2.64	1.38	1.24	1.58	---	---	1.77
M	1.57	---	---	---	1.86	1.36	1.59	1.72	---	---	1.62
Phoenix Islands:											
S	2.33	4.09	1.63	1.80	1.85	2.20	1.50	2.53	2.59	2.15	2.08
M	2.30	4.45	2.02	2.59	2.00	2.49	1.70	2.57	4.10	1.99	2.21
L	1.93	3.22	2.22	1.97	2.09	1.37	1.32	2.80	3.73	2.53	1.90
East Marshall Islands: L	1.45	3.78	2.08	1.97	1.41	1.03	1.04	1.58	2.54	2.57	1.30
Bikini Island: S	1.51	3.30	1.28	1.58	1.78	.84	1.10	2.41	2.18	---	1.53
East Caroline Islands:											
S	1.34	4.04	1.25	1.49	2.04	1.21	1.19	1.75	2.83	2.50	1.51
M	1.25	3.79	1.34	1.49	1.66	.93	.87	1.78	2.68	2.28	1.30
L	1.60	3.27	1.98	1.66	2.22	1.10	1.11	1.90	3.23	2.04	1.59
Central Caroline Islands:											
S	1.64	3.01	.90	1.50	1.61	1.37	1.74	3.14	3.32	2.93	1.90
M	1.31	3.91	1.52	1.56	2.05	1.41	1.52	2.48	2.93	2.51	1.75
L	1.97	3.63	2.46	2.07	2.23	1.48	1.52	3.13	3.72	3.13	2.07
Philippines:											
S	2.14	---	---	---	2.82	2.49	2.02	2.50	---	---	2.39
M	2.37	---	---	---	2.31	1.62	1.55	2.30	---	---	2.03
L	2.74	---	---	---	3.11	1.87	2.25	3.62	---	---	2.72
Japan: S	1.78	3.65	1.32	1.49	2.01	1.34	1.11	2.16	2.91	---	1.68
Hawaii:											
S	1.77	4.87	1.75	1.79	2.17	1.51	1.56	2.77	3.70	---	1.96
M	2.19	5.04	1.95	2.55	2.65	1.37	1.49	2.72	3.42	---	2.08
L	1.74	3.84	2.20	2.13	2.01	1.41	1.26	2.04	3.36	---	1.69
Hawaii:[5]											
S	1.52	---	---	---	1.70	1.01	1.05	1.98	---	---	1.45
L	1.32	---	---	---	2.03	1.20	1.05	1.51	---	---	1.42
Society Islands: S	1.49	4.12	1.60	1.97	2.42	1.43	---	---	---	---	1.78
Northeast Africa: S	2.19	3.90	1.53	2.08	2.92	1.93	1.87	2.98	2.52	---	2.38
Angola, Africa:[6]											
M	1.88	3.98	1.33	1.47	2.29	1.39	1.46	1.62	---	---	1.73
L	1.90	3.58	1.86	2.36	2.24	1.19	1.46	1.72	---	---	1.70
Means:											
S	1.72	3.86	1.42	1.69	2.06	1.39	1.32	2.22	2.94	2.56	1.74
M	1.84	3.97	1.82	2.09	2.09	1.48	1.43	2.19	3.39	2.26	1.81
L	1.88	3.68	2.24	2.28	2.21	1.34	1.32	2.30	3.26	2.65	1.81

---

[1] S, fish less than 80 cm., and compared at a length of 65 cm.; M, fish from 80 to 120 cm., and compared at a length of 100 cm.; L, fish more than 120 cm., and compared at a length of 140 cm.

[2] Mean of columns (1), (5), (6), (7), and (8).

[3] Godsil (1948) and in correspondence.

[4] Schaefer (1952).

[5] Godsil and Greenhood (1951).

[6] Schaefer and Walford (1950).

Of most interest, however, is the rather small amount of variation in the mean C values for the different samples. These values range from a low of 1.30, equal in the eastern Marshalls group L and the eastern Carolines group M, to a high of 2.72 in the Philippines group L. The Philippines group S and the northeast Africa group S are next highest. (I have no information on how these samples were collected and the factors that may have caused the higher values.) Among the POFI samples the highest (2.21) value is found in the Phoenix Islands group M.

When I tried to relate the mean C to the number of measurers and to the coverage of the sample in figure 8, I found little relation. The grand mean for one to three examiners is 1.62; for four to six examiners, 1.88; and seven or more, 1.92. The relation to length of sampling period is similar: for 1 to 9 days the mean is 1.64; for 10 to 19 days, 1.91; and for 20 or more days, 1.80.

None of this evidence is conclusive, but there appears to be a slight increase in the value of C, which is associated with increased time, greater number of measurers, or greater area sampled. I cannot segregate these factors, but because curvilinearity appears in some of Godsil's (1948) samples which were collected during only a few days, the samples taken on fewer than 10 different

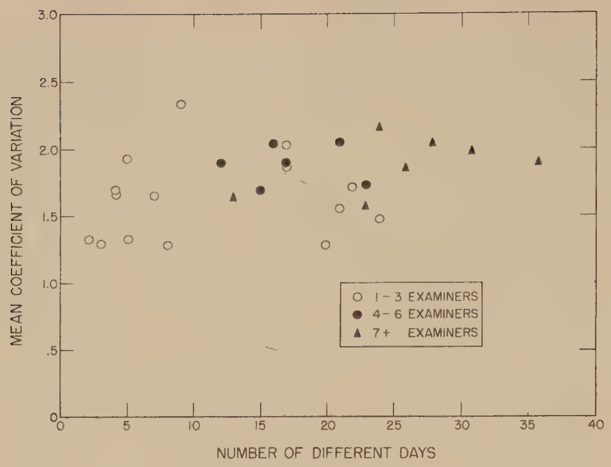

FIGURE 8.—Relation of the mean coefficient of variation of five selected characters to number of examiners and number of days on which parts of the sample were taken.

days may be less representative. Therefore, I conclude that important bias was not introduced by different techniques among measurers, at least not in the central and eastern Pacific area, where all of the measurers worked closely with one another.

CHARACTER-BY-CHARACTER COMPARISON OF SAMPLES

One of the most direct and useful ways of comparing morphological data is simply to compare the mean values estimated for certain fixed lengths. These values are particularly useful because they may be associated readily with geographic features and show directly the presence of character gradients or clines. Unlike tests of significance or amounts of overlap, an examination of the means shows directly the differences in number of parts or in body form. Of course, with all characters associated with body size it is necessary to control body size by the use of appropriate regressions.

A first comparison of samples is logically among the considerable series available from the equatorial Pacific. Areas from which these samples came extend from the American coast westward about 8,400 miles to the central Carolines area, which is bounded on the west by longitude 140° E. (fig. 2). This area of comparison is limited to the region between latitude 10° N. and latitude 10° S., although some of the samples are more restricted than this in latitudinal coverage. In the southern and extreme northern parts of this zone are the westerly flowing South Equatorial and North Equatorial Currents. Between these two currents (5° N. to 10° N.) is the easterly flowing Countercurrent. Throughout this area[6] yellowfin tuna have been taken near the Equator and have been found to be especially abundant between the Equator and the Countercurrent. They also have been found to be rather consistently scarce north of the Countercurrent and south of the Equator. They do, however, occur well to the north and south of this equatorial region, and no known barriers to their horizontal migration exist in any direction until water too cold for their liking is reached in the vicinity of latitude 40° N. or S.

So we know that the distribution of yellowfin is continuous from east to west in this equatorial band and that the tuna prefer a band about 300 miles wide in a north-south direction. Here is a situation where character gradients may be expected if the tuna are not freely intermingling across the whole equatorial Pacific.

In order to seek gradients I have adopted a slightly modified form of the method proposed by Hubbs and Hubbs (1953). Theirs is a graphical method in which the mean is plotted, a measure of dispersion is indicated by one standard deviation plotted on either side of the mean as a hollow bar, and a measure of reliability is indicated by two standard errors of the mean plotted as a solid bar on either side of the mean. The range is indicated by a base line. I have used comparable regression statistics, except for the range. First, the mean part size $\hat{Y}$ was calculated directly from the regression equation

$$\hat{Y}=a+bX.$$

Second, the dispersion around the regression line is indicated by one standard deviation from regression

$$S_{y\cdot x}=\sqrt{\frac{\Sigma y^2-(\Sigma xy)^2/\Sigma x^2}{n-2}}$$

plotted as a hollow bar on either side of the mean. The reliability of the mean is indicated by two standard errors of the mean estimated from regression

---

[6] In the gap between longitude 109° W. and the American coast (fig. 2), yellowfin have been taken by commercial vessels and research ships sponsored by the Inter-American Tropical Tuna Commission.

$$2S_{\hat{y}\cdot x}=2S_{y.x}\sqrt{1/n+x^2/\Sigma x^2}$$

plotted as a solid bar on either side of the mean.

These statistics were computed separately for each size group in each sample. For the small (S) group they were computed at a fork length of 65 cm., for the medium (M) group at 100 cm., and for the large (L) group at 140 cm. The three size groups are shown separately for all samples in figures 9 to 18. In each graph the equatorial Pacific samples are arranged in order from east to west and the other samples are added at the bottom.

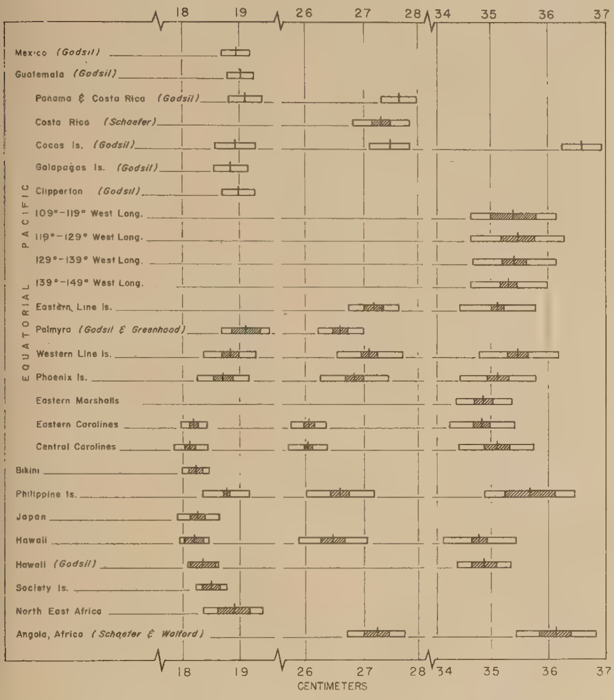

FIGURE 9.—Head length of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, solid bar ± two standard errors of the mean, hollow bar ± one standard deviation from regression.)

Almost all of the characters show gradients—sometimes stepped, sometimes continuous, and sometimes confused, perhaps because differences are small and sampling variation has its effect. The gradients, however, in most cases are unmistakable.

There is a distinct tendency toward shorter heads (fig. 9) in all three size groups from the western Pacific. The gradient is not smooth, because fish of the large group from longitude 109° W. to the western Line Islands area have much the same size head, and head size in the samples from the medium and small groups is much the same near the ends of the range.

The length of the pectoral fin (fig. 10) is distinctly greater in fish from the Caroline Islands area than in those from the eastern Pacific. Again similar tendencies occur in all size groups except

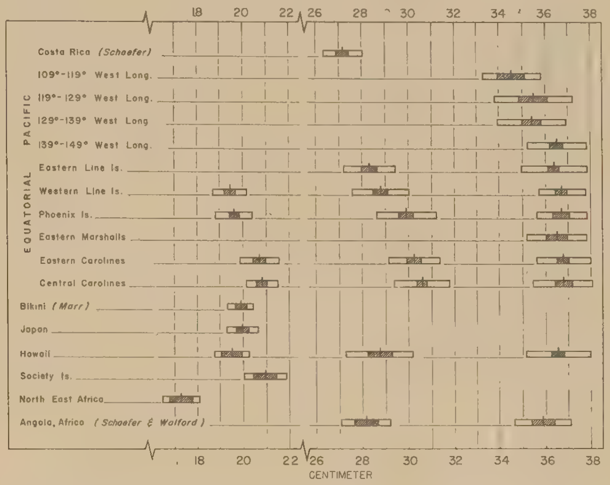

FIGURE 10.—Length of pectoral fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, solid bar ± two standard errors of the mean, hollow bar ± one standard deviation from regression.)

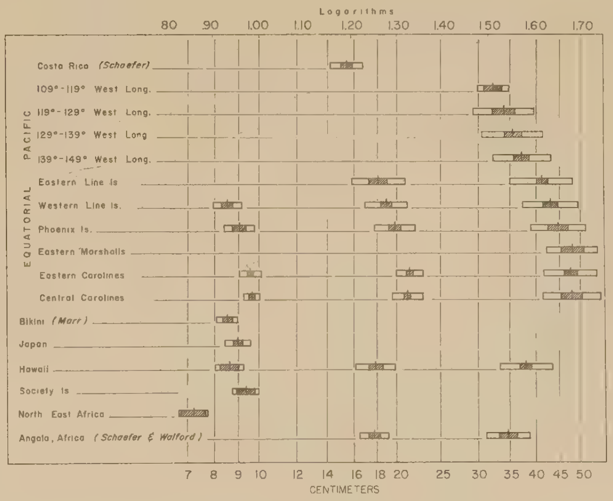

FIGURE 11.—Height of second dorsal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar ± one standard deviation from regression.)

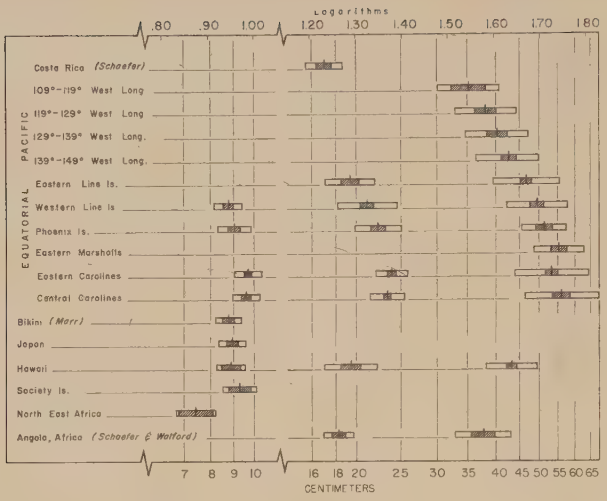

FIGURE 12.—Height of anal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar ± two standard errors of the mean, the hollow bar ± one standard deviation from regression.)

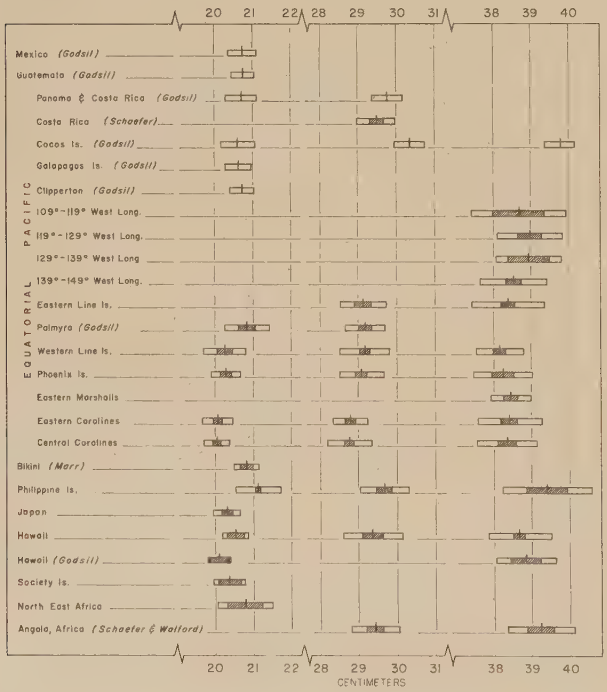

FIGURE 13.—Distance from snout to insertion of first dorsal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar ± two standard errors of the mean, the hollow bar ± one standard deviation from regression.)

that both the small and medium groups suggest a rather smooth cline, whereas the large group shows a rather similar fin length from longitude 139° W. to the Caroline Islands.

The differences in the height of the anal fin (fig. 12) and the height of the second dorsal fin (fig. 11) are even more marked, with clear and almost uniform gradients from the vicinity of Costa Rica to the eastern Marshalls and then about the same length fins on through the Caroline Islands area. Here the difference among samples of the large size group is about 16 cm. for height of second dorsal fin and 20 cm. for height of anal fin from longitude 109° W. to the Caroline Islands.

The distance between the snout and the insertion of the first dorsal fin (fig. 13) shows a distinct but somewhat irregular trend in the opposite direction, with the fish in the eastern Pacific having the greater measurement between these two points. In all size groups, insofar as samples are available, clearer trends in the same direction are to be noted in the measurements between the snout and the insertion of the second

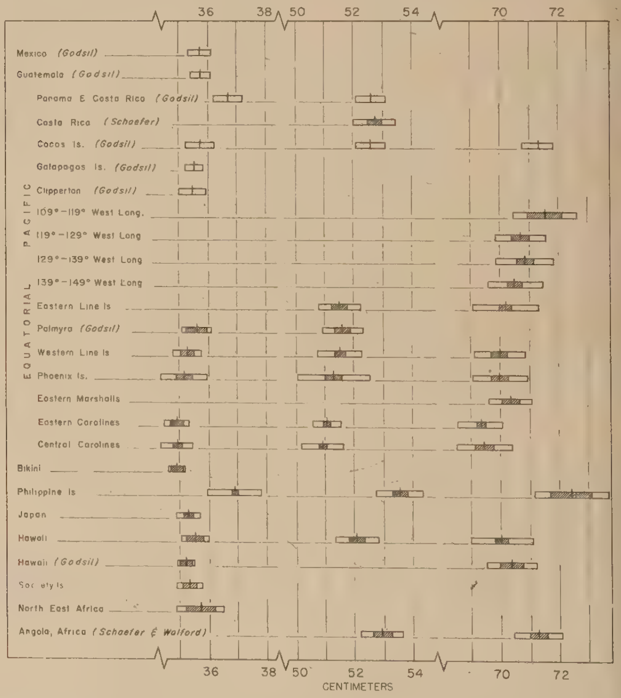

FIGURE 14.—Distance from snout to insertion of second dorsal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar ± two standard errors of the mean, the hollow bar ± one standard deviation from regression.)

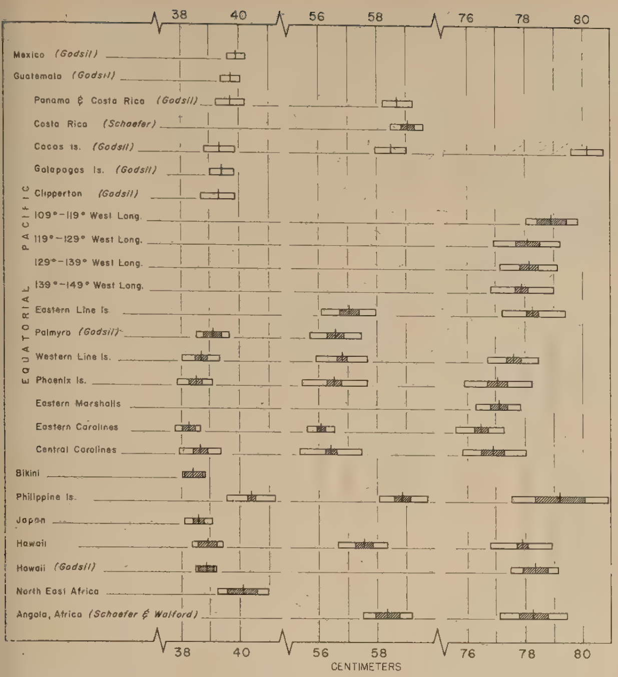

FIGURE 15.—Distance from snout to insertion of anal fin of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar ± two standard errors of the mean, the hollow bar ± one standard deviation from regression.)

dorsal fin (fig. 14) and between the snout and the insertion of the anal fin. In the large fish the trend is especially clearcut for the snout to insertion of anal fin (fig. 15). The snout to insertion of ventral fins (fig. 16) shows a somewhat similar tendency, but again the differences are smaller and sampling variation causes some confusion. The remaining characters, distance from the insertion of the ventral fins to the anterior edge of the vent (fig. 17) and greatest body depth (fig. 18), present a more confused picture. In the medium-sized fish there is a tendency for the fish from the eastern Pacific to have a greater body depth, but this tendency is not so noticeable among the larger specimens. The distance from the ventral insertion to the anterior edge of the vent divides the samples into two groups. The distance is about 40 cm. in the large size group among all samples from between longitudes 109° W. and 149° W. and about 39 cm. in the samples from the eastern Line Islands to the central Caroline Islands area.

Clearly, then, a more or less steady cline from the eastern to the west-central Pacific exists, with the average yellowfin in the eastern Pacific having the larger head, shorter pectoral, second dorsal, and anal fins, and greater distances from the snout to the insertions of first dorsal and ventral fins. It also has considerably the greater distances from the snout to the insertion of the second dorsal and anal fins, a greater body depth, and greater length from the ventral fins to the vent. Evidently, these greater distances to the insertions of the second dorsal and anal fins mean a correspondingly shorter caudal peduncle.

When this series of samples from the equatorial Pacific is compared with other samples from the more temperate waters some surprising differences are found. In the Bikini Island sample, which came from just outside the equatorial area at latitude 12° N., the fish would be expected to resemble those from the nearby Caroline Islands to the southwest, but they had especially short second dorsal and anal fins and a greater distance from the snout to the insertion of the first dorsal fin. The Bikini fish were small and were taken by trolling close to the island. In many regions of the Pacific these small yellowfin appear to be

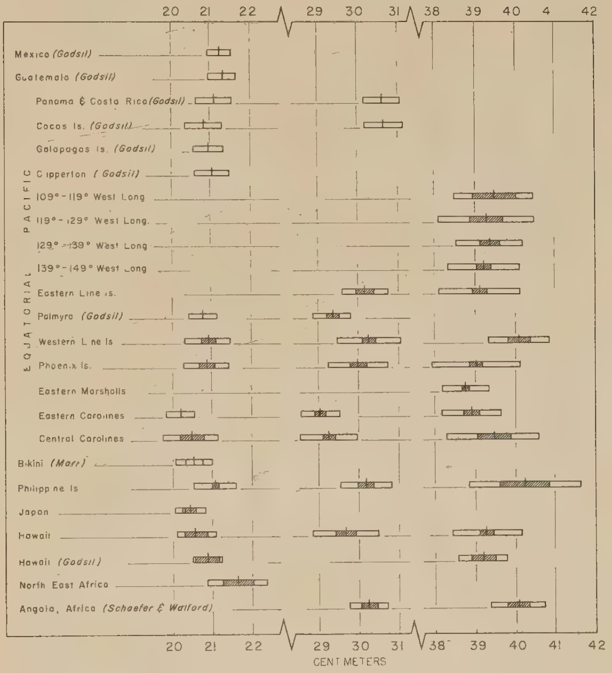

FIGURE 16.—Distance from snout to insertion of ventral fins of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar ± two standard errors of the mean, the hollow bar ± one standard deviation from regression.)

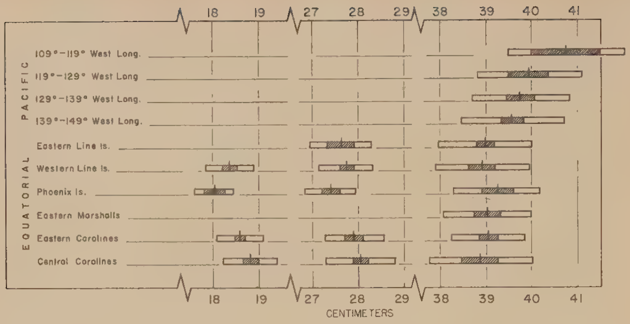

FIGURE 17.—Distance from insertion of ventral fin to anterior edge of vent of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar ± two standard errors of the mean, the hollow bar ± one standard deviation from regression.)

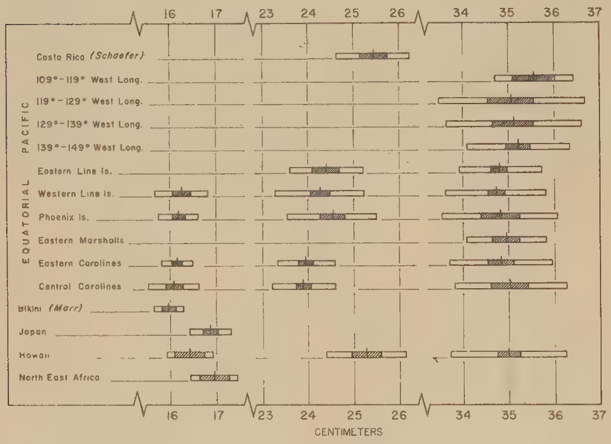

FIGURE 18.—Greatest body depth of small (65 cm.), medium (100 cm.), and large (140 cm.) yellowfin tuna, as estimated from regression statistics. (The center line indicates the mean, the solid bar ± two standard errors of the mean, the hollow bar ± one standard deviation from regression.)

common in the vicinity of islands and are very rarely taken on longlines. So this group of small fish near Bikini may be a relatively isolated one.

Characteristics of the sample from the Philippines are particularly surprising, because in all of the characters examined the fish are much more like those of the eastern Pacific than those of the nearby Caroline Islands area. This is consistently true for all size groups in all characters. Further, in the distance from the snout to the insertion of the first dorsal fin and also to the second dorsal, the means for the Philippine sample are distinctly larger than for any other samples.

The sample from Japan consisted only of small fish and in all respects is remarkably like the groups sampled from Hawaii. In not a single character is the difference of the means great enough to separate the dark bars that represent twice the standard error of the mean and, hence, indicate a statistically significant difference between the means.

The samples from Hawaii show somewhat mixed relationships with those from the equatorial area. In head length they are similar to those from the Caroline Islands, whereas in length of fins and in the distances from snout to insertion of the second dorsal and anal fins they are much more like the yellowfin of the equatorial area southeast of Hawaii between longitudes 129° and 159° W.

The sample of small yellowfin from the Society Islands was measured after being landed and thawed in Honolulu. Such handling may have changed the dimensions and this sample may not be directly comparable to the others. For this reason this is not a satisfactory sample. It is, however, near the Phoenix Islands sample in head length, height of the anal fin and distances from snout to first and second dorsal fins, but it has a very short second dorsal fin and much longer pectoral and anal fins than any other sample.

The sample from off Somaliland in northeast Africa is the most diverse of the group. It is similar to one or more central Pacific equatorial samples in head length and distances from snout to insertion of first and second dorsal fins, but it has very short pectoral, second dorsal, and anal fins. Somaliland fish also have a very long distance from the snout to the insertion of the anal fin, an especially deep body, and a long distance from the snout to the insertion of the ventral fins. This sample is very different from the sample from the west coast of Africa taken near Angola, where the fish are remarkably similar to those of the eastern Pacific in most dimensions. The yellowfin from Angola differ from those from Costa Rica principally in having slightly longer fins (as was pointed out by Schaefer and Walford, 1950).

In summary, yellowfin from the Pacific show a continuous cline morphologically along the Equator, whereas the samples taken in areas distant from the Equator differ erratically from the equatorial cline. The dimensions, however, are within the range of characters in the equatorial cline or are so close to one of the ends of the cline that there appears to be no evidence of genetically isolated stocks in the Pacific. This evidence will be considered further after data on overlap have been discussed.

COMPARISON OF SAMPLES FROM THE SAME AREA

Samples by Godsil (1948) and Godsil and Greenhood (1951) were obtained from areas also sampled by Schaefer and Walford (1950) or by POFI, and it is useful to look for evidence that different methods of measurement may have been used. Godsil's sample from Panama and Costa Rica came from an area close to that of Schaefer and Walford's from Costa Rica, and agreement among the four characters available for comparison is generally good even though Godsil's fish have slightly longer heads and a slightly longer distance from the snout to first dorsal fin. In addition, Godsil's sample from Hawaii may be compared with that of POFI, for it was obtained from rather limited areas: the small fish came from near Johnston Island and off islands between Kauai and French Frigate Shoals and the large fish from the Honolulu fish market. The POFI sample was obtained from a much wider area, although again most of the large fish were measured in the Honolulu market. Five measurements in two size groups are available to compare, and in not a single instance is the difference between means great enough to separate the black bars (and indicate a statistically significant difference).

Not as close statistically are Godsil and Greenhood's samples from Palmyra Island and the POFI samples from the eastern and western Line Islands, but the differences are complicated. Samples are available for comparison of small and medium size yellowfin taken by Godsil and Greenhood with similar sizes taken by POFI from the western Line Islands and a sample of medium size yellowfin from the eastern Line Islands. Godsil and Greenhood's data from Palmyra Island were obtained from frozen fish in a catch made during about 12 days of fishing in the vicinity of Fanning and Palmyra Islands. These days were nearly consecutive during February 1949. The POFI samples of small and medium fish were obtained from these islands as well as in the vicinity of the neighboring Washington and Christmas Islands, Kingman Reef, and a few from farther offshore. (All of these islands are near the borderline between our eastern and western Line Islands areas.) They were, however, taken over a much longer period (table 2) so they should be much more representative of the areas than Godsil and Greenhood's samples.

When a comparison of the mean character sizes of group M fish is made between our eastern and western Line Islands samples, not a single character differs by more than the length of the black bars, except height of the anal fin, and here the difference is in line with the general trend along the Equator. But when these two samples and the sample of small yellowfin from the western Line Islands are compared with Godsil and Greenhood's sample, I find that in head length their group M runs smaller and their group S somewhat larger; in distance from snout to insertion of first dorsal fin, their group M is about the same, and their group S considerably larger. Their distances from snout to insertions of second dorsal and anal fins show fairly good agreement with POFI samples. In the last character—distance from snout to insertion of the ventral fins—there is fairly good agreement between Godsil and Greenhood's sample and the POFI sample from the western Line Islands for group S; but then for group M the distance is markedly shorter than in either of the other two samples. Such erratic results suggest either that Godsil and Greenhood may have been sampling too few schools of fish to obtain a thoroughly representative sample or that freezing and thawing may have changed the proportions of the fish.

Despite these differences, I conclude that the techniques of measurement used by POFI were sufficiently close to those used by Godsil and Greenhood to arrive at about the same conclusions with regard to morphological differences among yellowfin from different areas of the Pacific.

MULTIPLE CHARACTER COMPARISON

After having examined the data for the mean differences in body shape, I shall consider next the overlap of the frequency distributions not merely of one character but of all characters considered simultaneously.

The measure of overlap that I shall use is similar to the measures of overlap used by taxonomists in many fields (Mayr et al., 1953: 146). The measures have all arisen from the concept of two overlapping frequency distributions and are expressed either as the percent of the actual frequency classes in the area of overlap or as a proportion of the observations estimated to be in the area of overlap of two normal distributions. The amount of overlap can be indicated as the distance between the means in units of the standard deviation or as an area under the curves. I prefer a measure of the overlapping area under two normal curves, which I have described fully (Royce, 1957) and which I have called Ω. The overlap (Ω) is expressed as a percent and varies from 0 to 100 as the means of the distributions approach one another.

This concept of overlap is especially useful because it answers the question, "What parts of population *A* possess characters that are within the range of population *B*?" I shall construe the answer to this question as a maximum for the proportion of population *A* which might have migrated from the area of population *B*.

In the computational procedure I shall follow closely the method outlined by Rao (1952, chapters 8 and 9). His method starts with pooled estimates of the correlations and standard deviations which are applied to the normalized mean values in order to transform them to values that are uncorrelated and that have unit standard deviations. In this method of analysis the amount of work increases approximately as the square of the number of characters used. To reduce the number, we have dropped from further consideration the greatest body depth, the distance from insertion of ventral fin to anterior edge of vent, and the distance from snout to insertion of ventral fins. This procedure seemed justifiable because (1) in some of our samples one or more of these characters were not measured, (2) none of them revealed as large differences between areas as other characters, (3) the distance from snout to insertion of ventral fins is highly correlated with head length and distance from snout to insertion of anal fin, and (4) it will be shown subsequently that seven characters are probably more than are necessary.

Because the statistics have arisen from regression analysis, it will be necessary to substitute for Rao's statistics comparable statistics determined from regression. Instead of the intragroup standard deviations from the mean, I use the intragroup standard deviations from regression. Instead of the intragroup correlations of the several characters, I use the intragroup partial correlations independent of total length. Instead of the actual mean values of the characters, I use the mean values estimated for certain given fork lengths. Therefore, in all of the statistics the effect of any changes with fork length is removed.

It has been impossible to assume that the regression lines were satisfactory beyond limited length groups, so we have broken down all of our statistics (except for partial correlations) into the length groups which were used in the previous section for character-by-character comparisons. They are group S, composed of fish less than 80-cm. fork length, which are compared at a length of 65 cm. (about 12 lb.); group M, from 80 to 120 cm., compared at a length of 100 cm. (43 lb.); and group L, more than 120 cm., compared at a length of 140 cm. (118 lb.). The basic regression constants, means, et cetera are in the appendix.

Because adequacy of the sampling varied widely, I have sought to obtain estimates of standard deviations from samples that I consider to be more representative. I have chosen the three areas most widely represented in time and among all three length groups; namely, Hawaii, western Line Islands, and eastern Caroline Islands. From these samples for each character in each size group I have obtained the standard deviation from regressions squared, $S_{y.x}^2$, averaged it for the three areas, and ended with an estimate of a pooled standard deviation from regression (within groups) which gives equal weight to the three areas (table 5).

TABLE 5.—*Pooled mean standard deviations from regression for each body character for the three size groups*

Size group (cm.)	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Small, <80	0.3981	0.7822	0.03163	0.03283	0.4470	0.5990	0.5897
Medium, 80–120	.5903	1.2891	.04626	.06141	.6776	.9426	.8943
Large, >120	.6596	1.2280	.06011	.05680	.7576	.9581	.9614

These standard deviations are the basic units of morphological distance, and it is desirable to examine them to determine how representative they are of all samples. Two matters are pertinent: first, I have used the actual standard deviation from regression without adjusting for the difference of the mean $\bar{x}$ from the X used for comparisons, so I need to know how close the means are to the comparison values; and second I need to consider whether the average dispersion about the lines is close to the grand average of all samples. The mean lengths of the three areas (giving equal weight to each) are 62.10, 99.32, and 142.04 cm. The means chosen for comparison are 65, 100, and 140 cm. If we consider that the standard deviation is directly proportional to the length of fish, then I have tended to underestimate slightly the standard deviation for the small and the medium groups and have slightly overestimated it for the large group.

In addition, the standard deviation of $\hat{Y}$ increases with distance from $\bar{y}$. For this reason I have tended to slightly underestimate the $S_{y.x}$ for the small and large groups.

Finally, the average coefficients of variation (table 4) of the three selected areas (for five characters) for the three size groups are 1.85, 1.80, and 1.63. These coefficients are close to the grand means of all samples, which are 1.74, 1.81, and 1.81 for small, medium, and large groups, respectively. With these partly compensating and in all cases small differences, I have chosen to make no adjustments but used the standard deviations from regression directly with confidence that they are very close to the grand average.

For the partial correlations of the several characters independent of fork length I have used a selected sample of 30 fish each from Hawaii, Costa Rica, eastern Line Islands, western Line Islands, and central Carolines. The 30 fish were selected from each area in the size range from 80 to 130 cm. and were chosen at random within the size group. From these, the intragroup correlations (table 6) and partial correlations were calculated (table 7).[7]

From the means and the pooled standard deviations the normalized mean values of each character have been obtained. The means were simply averaged to obtain a grand average, and then the deviations of each mean from the grand average in units of the average standard deviation were found (table 8).

Using the notation of Rao (1952), the normalized mean values $x_1 \ldots x_p$ were then transformed to values $Y_1 \ldots Y_p$, which are uncorrelated, and subsequently to other values $y_1 \ldots y_p$, which have unit standard deviation. The general formulas as given by Rao are—

$$Y_p = x_p - a_{pp-1} - \ldots - a_{p1} Y_1$$

$$a_{ij} = \frac{b_{ij}}{V(Y_j)} \text{ when } j < i-1$$

$$b_{ij} = \lambda_{ij} - \sum_{t=j-1}^{1} a_{jt} b_{it}$$

$$V(Y_i) = \lambda_{ii} - \sum_{j=1}^{i-1} a_{ij} b_{ij}$$

$$y_i = \frac{Y_i}{\sqrt{V(Y_i)}}.$$

The a and b values (tables 9 and 10) are convenient intermediate values in the computations. $V(Y_i)$ (table 11) is the variance of Y_i and y_i and is the final transformed value of the normalized mean (table 12). From these transformed means which have unit standard deviation and which are uncorrelated with one another, I obtained the distance in units of the standard deviation squared (D^2) for each possible area comparison in each size group (table 13). The total D^2, obtained by adding the D^2 values for each of the seven characters, is subject to a small bias due to the number of characters and the size of the samples. This bias (which is largest in the smallest samples and most troublesome in the samples most closely related) is removed by subtracting the value

$$p \frac{n_1 + n_2}{n_1 n_2},$$

in which p is the number of characters and n_1 and n_2 the number of observations in each sample (Rao, 1952: 364).[8]

From the adjusted sum of D^2 the value of the overlap (Ω) is determined by finding D, then $\frac{D}{2}$, which is used as an argument to enter the tables of the area under a normal curve to find the area of one tail and then multiplying by 200 to express the area of two tails as a percentage Ω.

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[7] This table of partial correlations is one of the more laborious parts of the entire computation. The particular data were chosen during preliminary computations as a test of the method on rather widely dispersed groups, all with good sample coverage. The size group corresponds nearly but not exactly to size group M. I have assumed that the partial correlations of these body parts for what is essentially the medium-size group for five samples with wide coverage are the same for all areas and also for the small and large size groups.

[8] I have ignored the slight variation in value of n among different characters within the samples.

TABLE 6.—*Intragroup correlations of body characters*

[See text for explanations]

Character	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Fork length	0.98422	0.92124	0.93830	0.92534	0.97846	0.99448	0.99210
Head length		.90009	.92767	.91515	.98329	.98667	.98618
Length of pectoral fin			.92373	.89801	.89439	.90894	.90865
Height of—							
Second dorsal fin				.96177	.91393	.92877	.92584
Anal fin					.90770	.91479	.90931
Snout to insertion of—							
First dorsal fin						.98647	.97739
Second dorsal fin							.99074

TABLE 7.—*Partial correlations of body characters, independent of fork length*

Character	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Head length	1.0000	−0.0960	0.0683	0.0657	0.5549	0.4243	0.4387
Length of pectoral fin		1.0000	.4409	.3088	−.0873	−.1766	−.1088
Height of—							
Second dorsal fin			1.0000	.7133	−.0583	−.1199	−.1164
Anal fin				1.0000	.0292	−.1367	−.1833
Snout to insertion of—							
First dorsal fin					1.0000	.6191	.2571
Second dorsal fin						1.0000	.3131
Anal fin							1.0000

TABLE 8.—*Normalized mean values* x_i *of body characters*

Size group and area	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
SMALL-SIZE GROUP							
West Line Islands	0.9797	−0.3068	−0.2308	−0.1889	−0.2461	0.0334	−0.1187
Phoenix Islands	.6782	−.0511	.5185	.2315	−.2237	−.0334	−.5257
Bikini Island	−.5024	.2813	−.2940	−.1614	.9843	−.4841	−.5935
East Caroline Islands	−.5777	1.3424	1.2235	1.2489	−.7383	−.5175	−.8818
Central Caroline Islands	−.7284	1.5597	1.3468	1.0448	−.7383	−.4674	−.2035
Japan	−.3266	.3963	.3351	.1340	−.2013	.1669	−.2713
Hawaii	−.5526	−.1790	−.1676	−.0061	.3803	.5342	.2544
Northeast Africa	1.1304	−3.0043	−2.7347	−2.3089	.8725	.7846	2.3402
MEDIUM-SIZE GROUP							
Costa Rica	.8809	−1.4274	−1.7034	−1.3109	.4870	1.0397	2.0463
East Line Islands	.6776	−.5740	−.2810	−.3843	−.0443	−.2228	−.1565
West Line Islands	.5590	−.1164	.0843	.2215	0	−.2228	−.4137
Phoenix Islands	.1016	.7214	.5275	.6009	−.1033	−.5092	−.7045
East Caroline Islands	−1.2197	.9619	1.1911	1.0780	−.5313	−.7532	−1.3083
Central Caroline Islands	−1.2367	1.2411	1.1176	.9168	−.5756	−.8805	−.8722
Hawaii	−.5252	−.1551	−.4172	−.3713	.3542	.3395	.3466
Angola, Africa	.7623	−.6283	−.5275	.7572	.4280	1.2306	1.0846
LARGE-SIZE GROUP							
109°–119° W	.2122	−1.3029	−1.5339	−1.9894	.1320	1.2420	1.2690
119°–129° W	.3335	−.5130	−1.1429	−1.2993	.5280	.4175	.364
129°–139° W	.2426	−.5782	−.8285	−.8838	.4884	.5219	.4473
139°–149° W	.0910	.2524	−.5107	−.4806	−.0528	.1774	.2288
East Line Islands	−.2122	.1629	.2196	.2289	−.2640	−.1566	.5409
West Line Islands	.3487	.3502	.5523	.6954	−.5412	−.3862	−.1144
Phoenix Islands	−.2122	.3339	.7969	1.0000	−.4488	−.3549	−.6969
East Marshall Islands	−.5761	.2769	1.2610	1.4754	−.1584	−.0417	−.6553
East Caroline Islands	−.6216	.5375	1.3026	1.5933	−.2376	−1.0437	−1.3106
Central Caroline Islands	−.2274	.4805	1.3159	1.5827	−.3300	−.9498	−.8217
Hawaii	−.6822	.3013	−.3876	−.4947	.1188	−.2818	.1768
Angola, Africa	1.3190	−.2606	−1.0497	−1.4261	.8316	.9185	.5721

The results of these computations expressed as the percentage of overlap between areas appear in table 14. Here the equatorial series has been arranged in order from Costa Rica on the east to the central Carolines on the west. The other samples from Bikini Island, Japan, Hawaii, Angola, and northeast Africa are added in no special order.

TABLE 9.—*Table of* a

[See text for explanation]

Character	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Head length	1.0000	−0.0960	0.0633	0.6507	0.5549	0.4243	0.4387
Length of pectoral fin		1.0000	.45162	.31804	−.03435	−.13713	−.06731
Height of—							
Second dorsal fin			1.0000	.71415	−.10190	−.11033	−.14654
Anal fin				1.0000	.12486	−.11991	−.21979
Snout to insertion of—							
First dorsal fin					1.0000	.55912	.01926
Second dorsal fin						1.0000	.14781
Anal fin							1.0000

TABLE 10.—*Table of* b

[See text for explanation]

Character	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
Head length	1.0000	−0.0960	0.0683	0.0657	0.5549	0.4243	0.4387
Length of pectoral fin		1.0000	.44746	.31511	−.03403	−.13587	−.06668
Height of—							
second dorsal fin			1.0000	.56650	−.08083	−.08752	−.11625
Anal fin				1.0000	−.06129	−.05886	−.10790
Snout to insertion of—							
First dorsal fin					1.0000	.37742	.01300
Second dorsal fin						1.0000	.08478
Anal fin							1.0000

NOTE.—These values are recorded in 5 significant figures; however, 8 significant figures were carried in the computations leading to *a*-values. The first row was obtained by preceding computations to 4 significant figures.

TABLE 11.—*Variances and square roots of variances for various body measurements*

[See text for explanation]

Variate	Variance[1] $V(Y_i)$	$D\sqrt{V(Y_i)}$	Variate	Variance[1] $V(Y_i)$	$D\sqrt{V(Y_i)}$
$V(Y_1)$	1.00000	1.00000	$V(Y_6)$	.57360	.75736
$V(Y_2)$	.99078	.99538	$V(Y_7)$	.74952	.86575
$V(Y_3)$	.79325	.89065	$V(Y_8)$	.76599	.87521
$V(Y_4)$	.49090	.70064	$V(Y_9)$	.40215	.63415
$V(Y_5)$	.67503	.82160	$V(Y_{10})$	.33024	.57466

[1] Values are recorded in 5 significant figures; however, 8 significant figures were carried in the computations leading to *a*-values (in table 9).

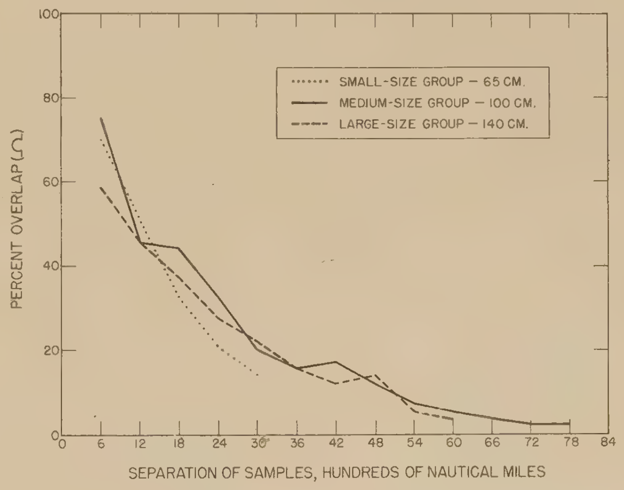

FIGURE 19.—Average percent of overlap of samples of yellowfin from the equatorial Pacific.

In the equatorial series there is a clear tendency for more closely located samples to have greater overlap. The overlap varies from a maximum of 82 percent and 81 percent in medium and large size groups for the comparison between eastern Carolines and central Carolines to a low of 3 percent for the comparison of Costa Rica with eastern Carolines and central Carolines. The relation of the average overlap to the separation of the samples in miles (fig. 19) is clear cut and much the same in all size groups. This graph has been made with the assumption that each population was located in the center of each 10° block of longitude and that the centers of these blocks were separated by units of 600 miles. (This assumption disregards the small variations in location within the sample areas and the fact that one sample area was 11° of longitude in width instead of 10°.)

From this graph it appears that, on the average, samples of yellowfin tuna from along the Equator separated by 1,500 miles overlap less than 50

TABLE 12.—*Transformed normalized mean values y_i of characters*

[See text for explanation]

Size group and area	Head length	Length of pectoral fin	Height of—		Snout to insertion of—		
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin
SMALL-SIZE GROUP							
West Line Islands	0.9797	−0.2137	−0.2209	−0.0644	−0.9877	0.0200	−0.6794
Phoenix Islands	.6782	.0141	.5269	−.2178	−.6483	.0159	−.8993
Bikini Island	−.5024	.2342	−.4126	.0855	1.4924	−1.2648	−.3236
East Caroline Islands	−.5777	1.2929	.7622	.5606	−.4301	.2953	−.4415
Central Caroline Islands	−.7284	1.4967	.8085	.1493	−.2710	.3465	.3585
Japan	−.3266	.3666	.2144	−.1384	.0293	.5073	−.1779
Hawaii	−.5526	−.2331	−1.0979	.2481	.7879	.5083	.5033
Northeast Africa	1.1304	−2.9092	−1.6824	−.5596	.5116	−.4330	1.6070
MEDIUM-SIZE GROUP							
Costa Rica	.8809	−1.3491	−1.2942	−.1691	−.1833	.5606	1.5185
East Line Islands	.6776	−.5113	−.1056	−.2852	−.5141	−.4994	−.5564
West Line Islands	.5590	−.0630	.0867	.2135	−.3933	−.3452	−.6631
Phoenix Islands	.1016	.7346	.2143	.3217	−.1744	−.4276	−.6604
East Caroline Islands	−1.2197	.8487	.9957	.3656	.2835	−.1604	−.5967
Central Caroline Islands	−1.2367	1.1276	.7736	.2127	.2444	−.2908	−.1059
Hawaii	−.5252	−.2065	−.3269	−.0907	.7508	.1975	.5458
Angola, Africa	.7623	−.5577	−.3650	−.5689	.0031	.9849	.5397
LARGE-SIZE GROUP							
109°–119° W	.2122	−1.2885	−1.0870	−1.2903	−.0190	1.0161	.7226
119°–129° W	.3335	−.4832	−1.0630	−.7023	.3547	−.1536	−.5763
129°–139° W	.2426	−.5575	−.6661	−.4276	.3794	.0888	.1557
139°–149° W	.0910	.2448	−.7034	−.1665	−.1755	.2241	.0757
East Line Islands	−.2122	.1432	.1894	.1100	−.1628	.0735	.7850
West Line Islands	.3487	.3855	.4008	.4218	−.8788	−.0040	−.1270
Phoenix Islands	−.2122	.3150	.7508	.6232	−.3732	.1000	−.4551
East Marshall Islands	−.5761	.2226	1.3444	.8387	.2648	.4147	−.1544
East Caroline Islands	−.6216	.4800	1.2644	.9676	.1873	−.7855	−.7008
Central Caroline Islands	−.2274	.4608	1.2610	.9273	−.1883	−.6629	−.3540
Hawaii	−.6822	.2369	−.5063	−.2895	.5901	−.4029	.4817
Angola, Africa	1.3190	−.1346	−1.2044	−1.0049	.0897	.1274	−.3964

percent in the seven characters considered; those separated by 3,000 miles overlap less than 25 percent; and those separated by 6,000 miles overlap less than 6 percent.

The graph also shows that the average overlap varies little with the size group of fish, although the data in table 14 indicate a slight tendency for the small and medium size groups to have less overlap than the large. This tendency appears to be most marked in the comparisons of samples from the western Line and Phoenix Islands areas with those from the eastern and central Caroline Islands areas. In all of these comparisons the large size group shows the most overlap and the small size group the least. In the comparisons of the Hawaiian samples with those from the equatorial area, the small size group shows the least overlap, but the medium size group generally shows slightly greater overlap than the large. The data are too scant to establish the significance of this tendency, but it may be associated with more wandering by the larger fish.

The overlap of the other samples with those from the equatorial Pacific area follows, in general, the relations that were deduced from consideration of single characters. The Bikini Island sample shows rather little overlap with any of the equatorial samples—even the sample from the nearby Caroline Islands area—but a considerable overlap with samples from Japan and Hawaii. The Japanese sample, on the other hand, is apparently intermediate in structure between the Bikini Island and equatorial samples, for it shows a considerable overlap with all other samples where a comparison is possible. The samples from Hawaii, likewise, show a fairly large amount of overlap with most of the equatorial samples, but the largest size group is most similar to the equatorial yellowfin from between longitudes 129° and 159° W. This area is generally southeast of Hawaii rather than directly south. The Angola, Africa, fish show a large amount of overlap with the large fish from longitudes 119° to 149° W. They are as similar to these fish as are many of the samples from adjoining areas along the Pacific Equator. Moreover, in all comparisons of Angola samples with samples from 119° to 149° W. there is a marked tendency for the overlap to be less among the larger size group than the medium size group. This finding conforms with the observation made by Schaefer and Walford (1950) that the principal characters differentiating

TABLE 13.—*Value of D^2 computed from transformed means and adjusted for sample size to determine percentage of overlap* (Ω)

Size group and area	Head length	Length of pectoral fin	Height of—		Snout to insertion of—			D^2	Bias	Adjusted D^2	Ω
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin				
SMALL-SIZE GROUP											
West Line-Phoenix Islands	0.0909	0.0519	0.5592	0.0235	0.1152	0.0000+	0.0484	0.8891	0.3482	0.5409	71
-Bikini Island	2.1966	.2006	.0367	.0225	6.1509	1.6507	.1266	10.3846	.3849	9.9997	11
-East Caroline Islands	2.4255	2.2698	.9665	.3906	.3109	.0758	.0566	6.4957	.2758	6.2199	21
-Central Caroline Islands	2.9176	2.9255	1.0597	.0457	.5137	.1066	1.0772	8.6460	.3482	8.2978	15
-Japan	1.7064	.3367	.1895	.0055	1.0343	.2375	.2515	3.7614	.3849	3.3765	36
-Hawaii	2.3479	.0004	.7691	.0977	3.1528	.2384	1.3988	8.0051	.3535	7.6516	17
-Northeast Africa	.0227	7.2657	2.1360	.2452	2.2479	.2052	5.2276	17.3503	.3049	17.0454	4
Phoenix-Bikini Islands	1.3938	.0484	.8827	.0920	4.5826	1.6402	.3314	8.9711	.4150	8.5561	14
-East Caroline Islands	1.5773	1.6353	.0554	.6059	.0476	.0781	.2096	4.2092	.3059	3.9033	32
-Central Caroline Islands	1.9785	2.1981	.0793	.1348	.1424	.1093	1.5821	6.2245	.3784	5.8461	23
-Japan	1.0096	.1243	.0977	.0063	.4591	.2415	.5204	2.4589	.4150	2.0439	47
-Hawaii	1.5149	.0611	2.6400	.2171	2.0627	.2748	1.9673	8.7379	.3836	8.3543	15
-Northeast Africa	.2045	8.5457	4.8810	.1168	1.3454	.2015	6.2815	21.5764	.3350	21.2414	2
Bikini-East Caroline Islands	.0057	1.1208	1.3802	.2257	3.6960	2.4339	.0139	8.8762	.3425	8.5337	14
-Central Caroline Islands	.0511	1.5939	1.4911	.0041	3.1096	2.5963	.4653	9.3114	.4150	8.8964	14
-Japan	.0309	.0175	.3931	.0501	2.1407	3.1403	.0212	5.7938	.4516	5.3422	25
-Hawaii	.0025	.2184	.4696	.0264	.4963	3.1439	.6838	5.0409	.4203	4.6206	28
-Northeast Africa	2.6660	9.8810	1.6124	.4162	.9620	.6919	3.7272	19.9567	.3716	19.5851	3
East Caroline-Central Caroline Islands	.0227	.0415	.0021	.1692	.0253	.0026	.6400	.9034	.3059	.5975	70
-Japan	.0631	.8580	.3001	.4886	.2110	.0449	.0695	2.0352	.3425	1.6927	51
-Hawaii	.0006	2.3287	3.4600	.0977	1.4835	.0454	.8926	8.3085	.3111	7.9974	16
-Northeast Africa	2.9176	17.6576	5.9761	1.2548	.8868	.5304	4.1964	33.4197	.2625	33.1572	.4
Central Caroline Islands-Japan	.1614	1.2771	.3530	.0828	.0902	.0259	.2877	2.2781	.4150	1.8631	49
-Hawaii	.0309	2.9922	3.6344	.0098	1.1213	.0262	.0210	7.8358	.3836	7.4522	17
-Northeast Africa	3.4551	19.4120	6.2046	.5025	.6125	.6076	1.5588	32.3531	.3350	32.0181	.4
Japan-Hawaii	.0511	.3596	1.7221	.1494	.5755	.0000+	.4640	3.3217	.4203	2.9014	39
-Northeast Africa	2.1228	10.7309	3.5979	.1774	.2326	.8842	3.1859	20.9317	.3716	20.5601	2
Hawaii-Northeast Africa	2.8325	7.1615	.3416	.6524	.0763	.8860	1.2182	13.1685	.3403	12.8282	7
ΣD^2	33.8002	101.3132	45.2911	6.3107	37.8848	20.1191	36.5245				
Mean	1.2072	3.6183	1.6175	.2254	1.3530	.7185	1.3044				
Σmeans	1.2072	4.8255	6.4430	6.6684	8.0214	8.7399	10.0443				
Ω	58	27	20	20	16	14	11				
MEDIUM-SIZE GROUP											
Costa Rica-East Line Islands	0.0413	0.7019	1.4128	0.0135	0.1094	1.1236	4.3052	7.7077	0.4535	7.2542	18
-West Line Islands	.1036	1.6541	1.9069	.1464	.0441	.8205	4.7594	9.4350	.3218	9.1132	13
-Phoenix Islands	.6073	4.3418	2.2756	.2409	.0001	.9765	4.7476	13.1898	.3600	12.8298	7
-East Caroline Islands	4.4125	4.8303	5.2436	.2859	.2179	.5198	4.4741	19.9841	.3686	19.6155	3
-Central Caroline Islands	4.4842	6.1340	4.2758	.1458	.1829	.7249	2.6387	18.5863	.3100	18.2763	3
-Hawaii	1.9771	1.3055	.9357	.0061	.8725	.1318	.9461	6.1748	.4473	5.7275	23
-Angola, Africa	.0141	.6263	.8634	.1598	.0347	.1800	.9580	2.8363	.5747	2.2616	45
East Line-West Line Islands	.0141	.2010	.0370	.2487	.0146	.0238	.0114	.5506	.2926	.2580	80
-Phoenix Islands	.3318	1.5523	.1023	.3683	.1154	.0052	.0108	2.4861	.3308	2.1553	46
-East Caroline Islands	3.5997	1.8496	1.2129	.4235	.6362	.1149	.0016	7.8384	.3394	7.4990	17
-Central Caroline Islands	3.6645	2.6860	.7730	.2479	.5753	.0435	.2030	8.1932	.2807	7.9125	16
-Hawaii	1.4467	.0929	.0490	.0378	1.6000	.4857	1.2148	4.9269	.4180	4.5089	19
-Angola, Africa	.0072	.0022	.0673	.0805	.2675	2.2031	1.2014	3.8292	.5454	3.2838	36
West Line-Phoenix Islands	.2092	.6362	.0163	.0117	.0479	.0068	.0000+	.9281	.1991	.7290	67
-East Caroline Islands	3.1638	.8312	.8263	.0231	.4581	.0342	.0044	5.3411	.2077	5.1334	26
-Central Caroline Islands	3.2245	1.4175	.4718	.0000+	.4067	.0030	.3105	5.8340	.1491	5.6849	23
-Hawaii	1.1755	.0206	.1711	.0925	1.3090	.2945	1.4614	4.5246	.2863	4.2383	30
-Angola, Africa	.0413	.2447	.2040	.6121	.1571	1.7692	1.4467	4.4751	.4138	4.0613	31
Phoenix-East Caroline Islands	1.7458	.0130	.6106	.0019	.2097	.0714	.0041	2.6565	.2459	2.4106	44
-Central Caroline Islands	1.7910	.1544	.3128	.0119	.1754	.0187	.3075	2.7717	.1873	2.5844	42
-Hawaii	.3929	.8857	.2929	.1701	.8560	.3908	1.4549	4.4433	.3245	4.1188	31
-Angola, Africa	.4365	1.6700	.3356	.7932	.0315	1.9952	1.4402	6.7022	.4520	6.2502	21
East Caroline-Central Caroline Islands	.0003	.0778	.0493	.0234	.0015	.0170	.2409	.4102	.1959	.2143	82
-Hawaii	.4823	1.1134	1.7493	.2082	.2184	.1281	1.3053	5.2050	.3332	4.8718	27
-Angola, Africa	3.9283	1.9780	1.8515	.8733	.0786	1.3117	1.2914	11.3128	.4606	10.8522	10
Central Caroline Islands-Hawaii	.5062	1.7798	1.2111	.0921	.2564	.2384	.4247	4.5087	.2745	4.2342	30
-Angola, Africa	3.9960	2.8402	1.2964	.6109	.0582	1.6274	.4168	10.8459	.4019	10.4440	11
Hawaii-Angola, Africa	1.6577	.1233	.0015	.2287	.5591	.6200	.0000+	3.1903	.5392	2.6511	41
ΣD^2	43.4554	39.7637	28.5558	6.1582	9.4942	15.8797	35.5809				
Mean	1.5520	1.4201	1.0199	.2199	.3391	.5671	1.2707				
Σmeans	1.5520	2.9721	3.9920	4.2119	4.5510	5.1181	6.3888				
Ω	53	39	32	30	29	26	21				
LARGE-SIZE GROUP											
109°-119° West-119°-129° W	.0147	.6485	.0006	.3457	.1397	1.3682	1.6871	4.2045	.4823	3.7222	33
-129°-139° W	.0009	.5344	.1772	.7443	.1587	.8599	.3214	2.7968	.4823	2.3145	45
-139°-149° W	.1469	2.3510	.1471	1.2629	.0245	.6273	.4185	4.9782	.3953	4.5829	28
-East Line Islands	.1801	2.0498	1.6292	1.9608	.0207	.8885	.0039	6.7330	.3779	6.3551	21
-West Line Islands	.0186	2.8023	2.2135	2.9313	.7393	1.0406	.7218	10.4674	.4540	10.0134	11
-Phoenix Islands	.1801	2.5712	3.3775	3.6615	.1255	.8392	1,3870	12.1420	.4855	11.6565	9
-East Marshall Islands	.6214	2.2834	5.9117	4.5326	.0805	.3617	.7691	14.5604	.5083	14.0521	6
-East Caroline Islands	.6952	3.1276	5.5291	5.0981	.0426	3.2458	2.0261	19.7645	.4583	19.3062	3
-Central Caroline Islands	.1932	3.0601	5.5131	4.9177	.0287	2.8190	1.1591	17.6909	.4306	17.2603	4
-Hawaii	.8000	2.3268	.3372	1.0016	.3710	2.0136	.0580	6.9082	.3860	6.5222	20
-Angola, Africa	1.2250	1.3315	.0138	.0815	.0118	.7898	1.2522	4.7056	.5926	4.1130	31

TABLE 13.—*Value of D^2 computed from transformed means and adjusted for sample size to determine percentage of overlap (Ω)*—Continued

Size group and area	Head length	Length of pectoral fin	Height of—		Snout to insertion of—			D^2	Bias	Adjusted D^2	Ω
			Second dorsal fin	Anal fin	First dorsal fin	Second dorsal fin	Anal fin				
LARGE-SIZE GROUP—continued											
119°–129° West-129°–139° W	0.0083	0.0055	0.1575	0.0755	0.0006	0.0588	0.5358	0.8420	0.2979	0.5441	71
-139°–149° W	.0588	.5300	.1293	.2871	.2811	.1427	.4251	1.8541	.2109	1.6432	52
-East Line Islands	.2978	.3924	1.5685	.6598	.2678	.0516	1.8531	5.0910	.1935	4.8975	27
-West Line Islands	.0002	.7546	2.1427	1.2636	1.5215	.0224	.2019	5.9069	.2696	5.6373	24
-Phoenix Islands	.2978	.6371	3.2899	1.7570	.5298	.0643	.0147	6.5906	.3011	6.2895	21
-East Marshall Islands	.8274	.4982	5.7956	2.3747	.0081	.3230	.1780	10.0050	.3239	9.6811	12
-East Caroline Islands	.9122	.9278	5.4168	2.7886	.0280	.3993	.0155	10.4882	.2739	10.2143	11
-Central Caroline Islands	.3146	.8911	5.4010	2.6556	.2948	.2594	.0494	9.8659	.2462	9.6197	12
-Hawaii	1.0316	.5185	.3099	.1704	.0554	.0622	1.1194	3.2674	.2016	3.0658	38
-Angola, Africa	.9712	.1215	.0200	.0916	.0702	.0790	.0324	1.3859	.4082	.9777	62
129°–139° West-139°–149° W	.0230	.6437	.0014	.0682	.3079	.0183	.0064	1.0689	.2109	.8580	64
-East Line Islands	.2068	.4910	.7319	.2890	.2940	.0002	.3960	2.4089	.1935	2.2154	46
-West Line Islands	.0113	.8892	1.1383	.7215	1.5831	.0086	.0799	4.4319	.2696	4.1623	31
-Phoenix Islands	.2068	.7613	2.0076	1.1042	.5664	.0001	.3731	5.0195	.3011	4.7184	28
-East Marshall Islands	.6703	.6086	4.0421	1.6035	.0131	.1062	.0962	7.1400	.3239	6.8161	19
-East Caroline Islands	.7468	1.0764	3.7268	1.9466	.0369	.7644	.7336	9.0315	.2739	8.7576	14
-Central Caroline Islands	.2209	1.0369	3.7137	1.8358	.3223	.5651	.2598	7.9545	.2462	7.7083	16
-Hawaii	.8553	.6311	.0255	.0191	.0444	.2418	.1063	1.9235	.2016	1.7219	51
-Angola, Africa	1.1586	.1788	.2898	.3333	.0839	.0015	.3048	2.3507	.4082	1.9425	49
139°–149° West-East Line Islands	.0919	.0103	.7971	.0765	.0002	.0227	.5031	1.5018	.1065	1.3953	55
-West Line Islands	.0664	.0198	1.2193	.3461	.4946	.0520	.0411	2.2393	.1826	2.0567	47
-Phoenix Islands	.0919	.0049	2.1147	.6236	.0391	.0154	.2817	3.1713	.2141	2.9572	39
-East Marshall Islands	.4450	.0005	4.1935	1.0104	.1939	.0363	.0529	5.9325	.2369	5.6956	23
-East Caroline Islands	.5078	.0553	3.8722	1.2861	.1316	1.0193	.6030	7.4753	.1869	7.2884	18
-Central Caroline Islands	.1014	.0467	3.8589	1.1964	.0002	.7868	.1846	6.1750	.1592	6.0158	23
-Hawaii	.5978	.0001	.0388	.0151	.5861	.3931	.1648	1.7958	.1146	1.6812	52
-Angola, Africa	1.5080	.1439	.2510	.7029	.0703	.0094	.2229	2.9084	.3212	2.5872	42
East Line-West Line Islands	.3146	.0587	.0447	.0972	.5127	.0060	.8317	1.8656	.1653	1.7003	51
-Phoenix Islands	.0000+	.0295	.3152	.2634	.0443	.0007	1.5378	2.1909	.1967	1.9942	48
-East Marshall Islands	.1324	.0063	1.3340	.5310	.1828	.1164	.8825	3.1854	.2196	2.9658	39
-East Caroline Islands	.1676	.1135	1.1556	.7355	.1226	.7379	2.2076	5.2403	.1696	5.0707	26
-Central Caroline Islands	.0002	.1009	1.1483	.6670	.0007	.5423	1.2973	3.7567	.1418	3.6149	34
-Hawaii	.2209	.0088	.4840	.1596	.5669	.2270	.0920	1.7592	.0972	1.6620	52
-Angola, Africa	2.3446	.0772	1.9427	1.2430	.0638	.0029	1.3957	7.0699	.3038	6.7661	19
West Line-Phoenix Islands	.3146	.0050	.1225	.0406	.2556	.0108	.1076	.8567	.2729	.5838	70
-East Marshall Islands	.8553	.0265	.8904	.1738	1.3078	.1753	.0751	3.5042	.2957	3.2085	37
-East Caroline Islands	.9415	.0889	.7458	.2979	1.1366	.6107	.3292	4.0706	.2457	3.8249	33
-Central Caroline Islands	.3319	.0057	.7399	.2555	.4768	.4341	.0515	2.2954	.2179	2.0775	47
-Hawaii	1.0628	.0221	.8228	.5059	2.1577	.1591	.3705	5.1009	.2476	4.8533	27
-Angola, Africa	.9415	.2705	2.5767	2.0355	.9380	.0173	.0726	6.8521	.3799	6.4722	20
Phoenix-East Marshall Islands	.1324	.0085	.3524	.0464	.4070	.0996	.0904	1.1361	.3272	.8089	65
-East Caroline Islands	.1676	.0272	.2638	.1186	.3142	.7841	.0604	1.7359	.2772	1.4587	55
-Central Caroline Islands	.0002	.0213	.2603	.0925	.0342	.5826	.6546	1.6451	.2494	1.3957	55
-Hawaii	.2209	.0061	1.5803	.8330	.9279	.2529	.8776	4.6987	.2048	4.4939	29
-Angola, Africa	2.3446	.2021	3.8228	2.6507	.2143	.0008	.0034	9.2387	.4114	8.8278	14
East Marshall-East Caroline Islands	.0021	.0663	.0064	.0166	.0060	1.4405	.2986	1.8365	.3000	1.5365	53
-Central Caroline Islands	.1216	.0567	.0070	.0078	.2053	1.1612	.0398	1.5994	.2722	1.3272	56
-Hawaii	.0113	.0002	3.4251	1.2728	.1058	.6685	.4046	5.8883	.2276	5.6607	23
-Angola, Africa	3.5914	.1276	6.4964	3.3989	.0307	.0825	.0586	13.7861	.4343	13.3518	7
East Caroline-Central Caroline Islands	.1554	.0004	.0000+	.0016	.1411	.0150	.1203	.4338	.2222	.2116	81
-Hawaii	.0037	.0591	3.1354	1.5803	.1622	.1464	1.3983	6.4854	.1776	6.3078	21
-Angola, Africa	3.7659	.3777	6.0950	3.8908	.0095	.8334	.0927	15.0650	.3843	14.6807	6
Central Caroline Islands-Hawaii	.2068	.0501	3.1233	1.4806	.6059	.0676	.6984	6.2327	.1498	6.0829	22
-Angola, Africa	2.3914	.3545	6.0782	3.7334	.0773	.6246	.0018	13.2612	.3565	12.9047	7
Hawaii-Angola, Africa	4.0048	.1380	.4873	.5118	.2504	.2812	.7711	6.4446	.3119	6.1327	22
ΣD^2	41.0543	37.1912	128.5601	78.4819	20.8264	29.4377	33.4614				
Mean	.6220	.5635	1.9479	1.1891	.3156	.4460	.5070				
Σ means	.6220	1.1855	3.1334	4.3225	4.6381	5.0841	5.5911				
Ω	69	59	38	30	28	26	24				

the Angola and Costa Rica samples—length of the pectoral fin and heights of the second dorsal fin and the anal fins—all have significantly higher regression coefficients in the Angola samples and diverge more from the Costa Rica sample in the larger size groups.

Lastly, the sample from northeast Africa shows little overlap with any other sample. Such is to be expected because of the marked differences in fin lengths and distance from the snout to the insertion of the anal fin, which have already been pointed out. However, it has also been mentioned that this sample from northeast Africa was not composed of yellowfin of a size strictly comparable to any of our size groups. Thus, much of these differences may have arisen because of the effects

TABLE 14.—*Percent of overlap (Ω) between areas, using seven characters*

Area and size group	109°–119° W.	119°–129° W.	129°–139° W.	139°–149° W.	East Line Islands	West Line Islands	Phoenix Islands	East Marshall Islands	East Caroline Islands	Central Caroline Islands	Bikini Island	Japan	Hawaii	Angola, Africa	Northeast Africa
Costa Rica: M	--------	--------	--------	--------	18	13	7	--------	3	3	--------	--------	23	45	--------
109°–119° W.: L	--------	33	45	28	21	11	9	6	3	4	--------	--------	20	31	--------
119°–129° W.: L	--------	--------	71	52	27	24	21	12	11	12	--------	--------	38	62	--------
129°–139° W.: L	--------	--------	--------	64	46	31	28	19	14	16	--------	--------	51	49	--------
139°–149° W.: L	--------	--------	--------	--------	55	47	39	23	18	23	--------	--------	52	42	--------
East Line Islands:															
M	--------	--------	--------	--------	--------	80	46	--------	17	16	--------	--------	19	36	--------
L	--------	--------	--------	--------	--------	51	48	39	26	34	--------	--------	52	19	--------
West Line Islands:															
S	--------	--------	--------	--------	--------	--------	71	--------	21	15	11	36	17	--------	4
M	--------	--------	--------	--------	--------	--------	67	--------	26	23	--------	--------	30	31	--------
L	--------	--------	--------	--------	--------	--------	70	37	33	47	--------	--------	27	20	--------
Phoenix Islands:															
S	--------	--------	--------	--------	--------	--------	--------	--------	32	23	14	47	15	--------	2
M	--------	--------	--------	--------	--------	--------	--------	--------	44	42	--------	--------	31	21	--------
L	--------	--------	--------	--------	--------	--------	--------	65	55	55	--------	--------	29	14	--------
East Marshall Islands: L	--------	--------	--------	--------	--------	--------	--------	--------	53	56	--------	--------	23	7	--------
East Caroline Islands:															
S	--------	--------	--------	--------	--------	--------	--------	--------	--------	70	14	51	16	--------	.4
M	--------	--------	--------	--------	--------	--------	--------	--------	--------	82	--------	--------	27	10	--------
L	--------	--------	--------	--------	--------	--------	--------	--------	--------	81	--------	--------	21	6	--------
Central Caroline Islands:															
S	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	14	49	17	--------	.4
M	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	30	11	--------
L	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	22	7	--------
Bikini Island: S	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	25	28	--------	3
Japan: S	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	39	--------	2
Hawaii:															
S	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	7
M	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	41	--------
L	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	22	--------

of curvilinear regressions, and I cannot say with confidence that this size group is as different as the data indicate.

EVALUATION OF MULTIVARIATE ANALYSIS

A full evaluation of the merits of the multivariate analysis which I have used here is beyond the scope of this article.[9] But the procedure is so laborious that some discussion of the value of considering extra characters is warranted. The labor increases approximately in relation to the square of the number of characters, but Mahalanobis, Majumdar, and Rao (1949) refer to Mahalanobis, Bose, and Roy (1937),[10] in which it is shown that D^2 approaches a limit as additional characters are considered. On an intuitive basis this would be expected to happen rather quickly, because as additional characters are considered they would have an increased chance of being correlated with previously considered characters. The extra amount of work involved in making the D^2 analysis is approximately related to the square of the number of characters considered, so the problem is how many characters must be considered to arrive at a reasonably stable estimate of overlap.

It can be shown readily that more than one character must be considered. To demonstrate this, I have taken 10 comparisons at random out of the total of 122 and calculated the overlap of the single characters showing the greatest difference between samples. These, I compared with the overlap computed from seven characters (table 15). In all but one [11] there is a substantial reduction in the overlap due to the extra characters. In fact, the single character comparison with the least overlap, that between eastern Marshalls and Angola with respect to height of the anal fin, still shows an overlap of 40 percent. This is reduced to 7 percent when six more characters are added.

The average effect of adding characters one by one may be obtained from the grand average, D^2, for each size group. These averages have been obtained from table 13 for each character and the overlap computed, first for one character, then two characters, and so on until the seven are considered. It may be seen (fig. 20) that most

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[9] A detailed evaluation of the application of D^2 to an anthropometric survey may be found in Mahalanobis, Bose, and Roy (1937).

[10] Not available to me.

[11] In this instance the seven characters show an overlap of 82 percent and the single character with the greatest difference shows an overlap of only 75 percent. This anomaly occurs because the other six characters when combined show less difference than the correction for small samples.

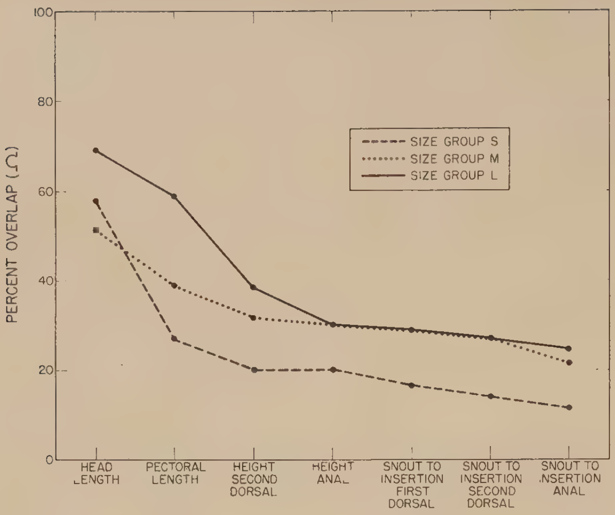

FIGURE 20.—Effect of adding characters on average overlap of all sample comparisons.

of the reduction (if any) in D^2 occurs in the first three or four characters, but that there is a continuing gradual reduction to the seventh character.

TABLE 15.—*Comparison of overlap of one character with overlap of seven characters considered simultaneously*

Sources of samples compared	Size group	Character showing greatest difference	Overlap (Ω)	
			1 character	7 characters
West Line Islands-Northeast Africa.	Small	Length of pectoral fin.	41	4
Bikini Island-Central Caroline Islands.	do	Height of second dorsal fin.	56	14
East Line Islands-Hawaii	Medium	Head length	59	19
East Caroline-Central Caroline Islands.	do	Snout to insertion of anal fin.	75	82
119°–129° West-East Line Islands.	Large	Height of anal fin.	54	27
129°–139° West-Phoenix Islands.	do	do	50	28
139°–149° West-Phoenix Islands.	do	do	55	39
Phoenix Islands-Hawaii	do	do	54	29
East Marshall Islands-Angola, Africa.	do	do	40	7
Hawaii-Angola, Africa	do	Head length	48	22

Another approach has been made in an examination of the character-by-character overlap of our most different, most similar, and moderately different equatorial samples (fig. 21). Here again it may be seen that in each case most of the reduction in overlap (if any) occurs in the first three or four characters.

It would also have been possible to improve the order in which I have considered the characters. The most useful characters are those that show the greatest difference among samples and the least correlation with other characters. Thus, a consideration of our character-by-character comparisons and the partial correlations of table 7 indicates that it would be desirable to consider height of the anal fin, which is one of the characters showing the greatest difference among samples, but not height of second dorsal fin, which is closely correlated with the height of the anal fin. For a similar reason I could have omitted the distance from the snout to insertion of the second dorsal fin after considering that of the snout to insertion of the first dorsal fin, with which it is highly correlated. Another rather high correlation exists between head length and distance from snout to insertion of first dorsal fin.

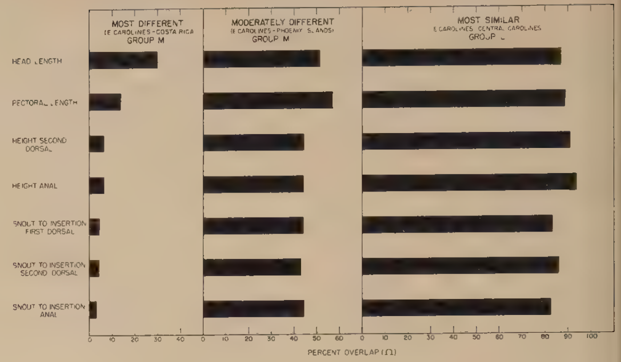

FIGURE 21.—Effect of adding characters on overlap of selected comparisons.

Thus, it would appear that had I considered only the best four characters, I would have found substantially the same overlap that I did in considering seven. This would have reduced the work of computation to about one-third of that for the seven characters. Rao (1952: 256) notes also that it is profitable to use samples of equal size.

EXTENT OF INTERMINGLING

As I have previously argued, the percentage of overlap of two samples may be considered to represent the maximum proportion of one sample that might belong to the other. When this concept is extended to two populations separated geographically, the overlap may be assumed to be the proportion of one which might have come from the other. There is, of course, no evidence that any part of the population did come from another, but the overlap may be used, together with other data, to estimate how much intermingling might be occurring.

Such use requires an assumption that the haracters selected to estimate the overlap are ixed. If the characters are genotypic and fixed ıt time of fertilization, then the overlap would ndicate a maximum amount of genetic mixing (gene flow). Many characters, however, are fixed luring early development and vary according to nvironment, especially temperature. Even so, he amount of overlap would still indicate a naximum possible amount of intermingling.

Clearly, between the two ends of the Pacific Equator the overlap is so small (3 percent) that here can be practically no intermingling. Along his long belt where the yellowfin distribution is continuous, I have previously noted that the average overlap is less than 50 percent in samples eparated by 1,500 miles and less than 25 percent n samples separated by 3,000 miles. Consequently, it seems probable that east-west migraion must be relatively limited and that most yellowfin tuna probably remain within a few hundred miles of where they occur as postlarvae. The eggs and larvae drift passively with the curents, but development is rapid and it seems ınlikely that they could drift more than 300 or 400 miles before becoming active swimmers.

I have noted previously that the average overlap among samples was about the same for the different ize groups. This clearly indicates that after hey reach a weight of about 5 pounds (50 cm.) here is no tendency for samples of the larger fish o become more diverse. Such evidence indicates hat the morphological differences arise very early n life and considering the similar environment in he surface layers along the Equator it seems probable that the differences are genotypic.

The samples from farther away from the Equaor—Bikini Island, Japan, and Hawaii—are sepaated from the Equator by a zone where yellowfin are relatively scarce. The Bikini sample shows ittle overlap with samples from the adjoining equatorial areas, much less in fact than with the Japanese sample. The Hawaiian sample shows ittle overlap with the smaller sizes from the equaorial areas, but the larger sizes are quite like hose from the Equator southeast of Hawaii. There is also considerable similarity between the Japanese sample and the Hawaiian sample.

The sample from Angola, Africa, has so much overlap with some of the equatorial Pacific samples that the maximum amount of intermingling might be large, but of course the geographic separation makes absurd the suggestion of any intermingling. In the case of the northeast Africa sample, both the markedly low overlap with all other samples and the geographic separation make the possibility of intermingling very small.

GEOGRAPHIC DISTRIBUTION OF YELLOWFIN

One kind or another of yellowfin tuna, genus *Neothunnus*, has been described from each of the warm seas of the world except the Mediterranean. Rosa (1950) has reviewed the extensive literature and noted that the distribution extends from Point Conception, California, to San Antonio, Chile, in the eastern Pacific; from Hokkaido, Japan, south through the Indonesian Archipelago to Cape Naturaliste, southwest Australia; around the shores of the Indian Ocean to the tip of South Africa; from French Equatorial Africa north to the coast of Portugal in the eastern Atlantic, and from Maryland in the United States south to the coast of Brazil in the western Atlantic. He also reported that yellowfin occur in the Red Sea, which is the warmest sea in the world, so the distribution extends from the warmest waters to those in the vicinity of latitudes 40° N. and 40° S.

To these coastwise records must be added the records of capture in the open Pacific far from land, as reported by Yōichi Yabuta in the Japanese atlas "Average Year's Fishing Condition of Tuna Longline Fisheries," from the exploratory fishing of POFI along the central and eastern Pacific Equator, in offshore records from the eastern Atlantic by Mather and Day (1954), and in the more recent unpublished records of the capture of yellowfin tuna in the open parts of the Gulf of Mexico and Caribbean Sea by exploratory fishing vessels. The Japanese atlas records the capture of yellowfin tuna along the Equator from longitude 170° W. to the Philippines, thence northward at various places to as far as latitude 43° N. along the coast of Japan, in all of the major seas of the southwest Pacific, and in the Indian Ocean in the vicinity of Sumatra and the Nicobar Islands.

This distribution corresponds quite closely to that of waters warmer than the 65° F. isothere (line of equal warming) shown by Hutchins and Scharff (1947). Along the coast of Chile the limit is between the 65° F. and the 60° F. isotheres, and in other areas the most poleward record is not quite to the 65° F. isothere. Further, no temperature barrier exists between any of the populations of yellowfin, for there is a broad band of summer temperatures between 65° F. and 70° F. around the Cape of Good Hope between the Atlantic and Indian Oceans.

Within the broad range of this species, however, there are widely varying concentrations. Already mentioned is the concentration along the Pacific Equator, where the yellowfin occur in an east-west band, and the scarcity in the open ocean north and south of this band. They do, however, occur in concentrations in the vicinity of many islands, in the Coral Sea off Australia, and possibly in other places separated from this equatorial belt by a region of yellowfin scarcity. The small yellowfin, in particular, seem to be concentrated fairly close to the islands, because they are rarely seen or caught on the high seas. The persistence of groups of these yellowfin along the reefs of certain islands has led to commercial fishing for them by trolling, and many fishermen feel that such yellowfin populations are relatively static. Thus, concentrations of yellowfin may vary enormously in extent from the clearly continuous distribution along many thousands of miles of the Pacific Equator to perhaps a relatively isolated group around a coral atoll.

Despite the variations in abundance, their widespread occurrence in all tropical oceans, near land and far from land, indicates that yellowfin tuna belong to the pelagic fauna of the warm seas and not merely to local faunal areas.

NOMENCLATURE

A great variety of scientific names has been assigned to yellowfin tuna in various parts of the world, and there has been no general agreement on the correct names to be assigned to the various species or subspecies. Rosa (1950) recognized three species: *Neothunnus albacora* (Lowe) 1839 of the eastern Atlantic Ocean, *N. argentivittatus* (Cuvier and Valenciennes) 1831 from the western Atlantic Ocean, and *N. macropterus* (Temminck and Schlegel) 1842 from the Pacific and Indian Oceans. Schaefer and Walford (1950) considered the Atlantic form to be *N. albacora* and the Pacific form to be *N. macropterus*. They designated a specimen from the Malabar coast of India as the lectotype of *N. argentivittatus*, and thus this name clearly applies to the Indian Ocean form unless it is decided that the Indian Ocean form should be the same species as one with a prior name from another ocean. Later Ginsburg (1953) considered that the name *Thunnus albacares* (Bonnaterre) 1788 was appropriate for the eastern Atlantic yellowfin, *T. subulatus* (Poey) 1875 for the western Atlantic yellowfin, *T. catalinae* (Jordan and Evermann) 1926 for the eastern Pacific yellowfin, and *T. macropterus* (Temminck and Schlegel) 1842 for the western Pacific yellowfin.

Rivas (1954: 316) referred in a footnote to Ginsburg's usage of *T. albacares* and accepted it as a valid name for all Atlantic yellowfin. Rivas (1961) reviewed the status of *T. albacares* again and opined that the various yellowfin populations from the Atlantic and the Pacific were not worthy of separate nomenclaturial recognition. He noted the widespread distribution in tropical waters and stated, ". . . it would seem therefore, that the yellowfin tuna represents a single pantropical species . . . ."

The characters that almost all authors have used to distinguish the species have been length of the pectoral fin and height of the second dorsal and anal fins. Ginsburg (1953) admits that the differences between the tuna of the eastern Atlantic and Hawaii (which he calls western Pacific) are only of racial magnitude and do not warrant separate names. He retained the separate names because he considered that (1) specimens of the two populations had not been directly compared, (2) not all promising phases of the morphology had been studied, (3) the tuna inhabit totally different faunal areas, and (4) most authors have treated the populations as distinct species. He, therefore, considered it desirable to avoid the confusion of shifting names in and out of synonymy.

Schaefer and Walford (1950) considered the differences between the eastern Pacific and eastern Atlantic forms sufficient to warrant separate species pending more information on the variability within oceans as compared with the variability between oceans. This information is now at hand from our studies and it shows clearly that the entire range of variation which has heretofore been used to describe the species of yellowfin occurs within one continuous distribution of yellowfin along the Pacific Equator. In fact, the differences between yellowfin from Costa Rica and from Angola (which Schaefer and Walford consider to be sufficient for a separate species) are much less than the differences between yellowfin from Costa Rica and the eastern Carolines. This difference between the Costa Rican and Caroline Islands yellowfin is far beyond the conventional level of a subspecific difference, but because of the clear evidence of continuous distribution and morphological gradients between these two areas the yellowfin from the two areas must be considered conspecific.

There also may be a similar cline across the tropical Atlantic. Ginsburg (1953) reviewed the scanty evidence which indicates that the western Atlantic form has longer second dorsal and anal fins than the eastern Atlantic form. If the cline is present, then the Atlantic forms, also, are conspecific.

If we add to this evidence the fact that the yellowfin is clearly a fish of the high seas and not restricted to any coastal faunal areas and the strong probability that the distribution is continuous in the oceans from the Pacific through the Indian to the Atlantic, all of the forms should be considered conspecific. The confusion can best be settled by reducing them to one species.

There will remain, of course, the possibility that certain yellowfin populations may be distinct enough to warrant a separate specific or subspecific name. This must be considered for the sample from northeast Africa off Somaliland, in which the fins are shorter than any we have found in the Pacific. However, our sample is not good, and with the evidence of continuous distribution through the Indian Ocean it seems most probable that this group is not completely separated from other yellowfin populations. Futhermore, it occurs in one of the warmest parts of the ocean, where the yellowfin would be expected to be the most different in structure.

Settling the matter of the proper specific name is only part of the problem. The generic name is also in dispute. Fraser-Brunner (1950) and Ginsburg (1953) used *Thunnus* rather than the long established generic name of *Neothunnus*. Godsil (1954) did not follow Fraser-Brunner but separated *Thunnus*, *Neothunnus*, and *Parathunnus*, principally on the basis of markings on the liver; however, he gives this problem of generic separation

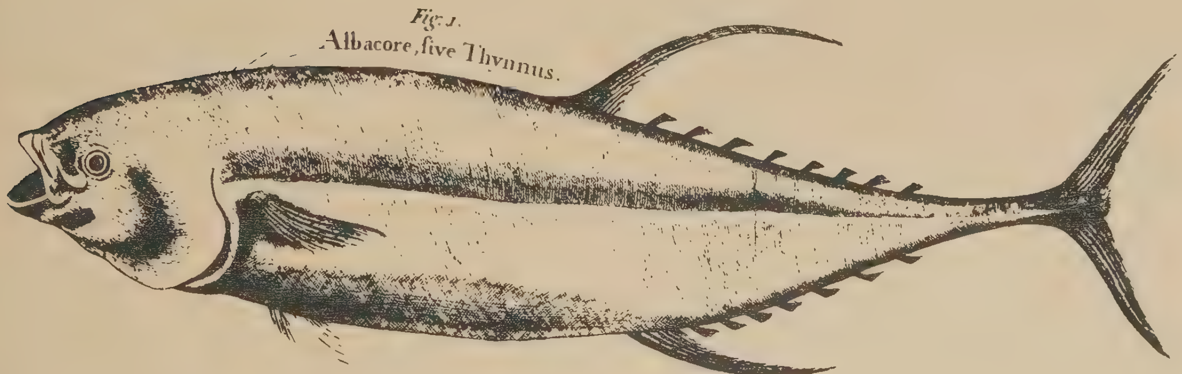
Fig. 1.
Albacore, ſive Thynnus.

FIGURE 22.—Figure of tuna from Sloane (1707) on which Bonnaterre's description (1788) was based.

little consideration. Fraser-Brunner reduced *Parathunnus* and *Neothunnus* to subgeneric status on the principle that a generic name is intended to express relationship. It is not desirable to have a group of monotypic genera. There is now no evidence to indicate that these genera should be separate, and so I follow Fraser-Brunner and Ginsburg, who use *Thunnus* for the bluefin, yellowfin, bigeye, and albacore group.

The final question is which specific name is correct. Schaefer and Walford (1950) considered that *T. argentivittatus* (Cuvier and Valenciennes) 1831 would have priority if only one species of yellowfin was recognized, but they did not discuss the merits of *T. albacares* (Bonnaterre) 1788. Ginsburg (1953) reviewed the question and concluded that the original figure of *albacares*, which shows the distinctive long second dorsal and anal fins of the yellowfin, must be considered a yellowfin even though the pectoral fin is too short. Bonnaterre's description of the yellowfin was based on a description and figure by Sloane (1707) which I reproduce here in full (fig. 22).

> The Sea hereabout is very well provided with *Albacores*, or *Thynni*, whose Description follows:
>
> ALBACORES DESCRIBED
>
> This Fish was Five Foot long from the end of the Chaps to that of the Tail, the Body was of the make and shape of a Mackerel, being roundish or torose, covered all over with small Scales, White in some places, and Darker colour'd in others, there was a Line run along each side. The coverings of the Gills of each side were made of two large and broad Bones covered with a shining Skin, the Jaws were about Six Inches long, having a single row of short strong sharp Teeth in them, and were pointed. The Eyes were large, and the Gills very numerous, behind which were a small pair of Fins. *Post anum* was a Foot long Fin, about Three Inches broad at bottom, and Tapering to the end. It had another on its Back answering that on the Belly, and from these were small *Pinnula* at every Two Inches distance to the forked Tail, which was like a New Moon falcated, before which on the Line of the two sides was a membranous thick horny Substance, made up of the Fishes Skin, stood out about three quarters of an Inch where it was highest, something like a Fin. It was about Three Foot Circumference a little beyond the Head, where it was thickest. The Eye was about an Inch and a half Diameter. The Figure of this Fish is here added, *Tab.* I. *Fig.* I. taken from a dried Fish, where every thing was perfect save the first Fin on the Back, which I suppose was accidentally rub'd off.
>
> It is frequently taken by Sailers with Fisgigs or White Cloath, made like Flying-Fish, and put to a Hook and Line for a Bait; The Flesh is coloured, and Tasts as the *Tunny* of the Mediterranean, from whence I am apt to believe it the same Fish. It is to be found not only about *Spain*, and in the way to the *West-Indies;* but in the South-Seas about *Guayaquil*, and between *Japan* and *New-Spain* every where.
>
> This is called *Tunnyes* of *Oviedo fum. p.* 214. *Albicores* of *Terry, p.* 9. *Albocores* of *Mandelflo, p.* 196. *Dolphin* or *Tunin of Marten, Orcynus Rondelet, p.* 249. *Thunnus Gesner.* 1158. *Aldrovand. p.* 307. *Mus. srammerd. Raii. Hist. p.* 176. *Tab. M.* I. *Corett. Thynni Species ejusd. app. p.* 5. & 24. *Tab.* 9. *No.* I. where the Figure seems not good. *Thynnus Bellon. p.* 106. *Salvian. p.* 124. *An palamite of Oviedo Sum. p.* 211? *Guarapucu Brasiliensibus, an Cavala Lusitanis, nostratibus Coninghvisch. Marcgr. p.* 178? *Pif. Ed.* 1658. *p.* 59? *vel an Curvata pinima ejusd. p.* 150? *Ed.* 1650. *p.* 51? *Tons* of *Escarbot Nova Francia, p.* 35. *du Raveneau de Lussan, p.* 171. *An Albacoretta Pis. Ed.* 1658. *p.* 73? *Toni di Fernan Colon vita di Christof. f.* 29. An Ox-Eye of *Anonymus Portugal. ap. Purchas, p.* 1313? *vel Toninas Ejusd. ib. p.* 1314? *Tunnies of Francis Gualle. Purchas,* 806. *Albacoras Ejusd. p.* 446. *Hakl.* of *Smith New-England, p.* 227. of *Galvanos Purchas,* in 42°. North Lat. South-Seas, *p.* 1685. *Ton ou tasard de Cauche, p.* 138. *An tonine Ejusd. p.* 142? *Ulasso* a Tuny Fish of *Duddeley. p.* 576. *Albacore* of *Ligon. p.* 6. *Abbeville. p.* 30. *An* a *Spanish* Macquerel of *Ligon*? *Albachores Pyrard. de Laval. p.* 6. 137.

A tuna of the size of Sloane's specimen almost certainly must have been one of either the yellowfin or the bluefin group. A comparison of measurements of Atlantic bluefin, Angola yellowfin, and Sloane's figure (table 16) indicates that Sloane's figure is closer to the yellowfin than to the bluefin in all characters except length of the pectoral fin. Further, Sloane's figure was taken from a dried fish from which the first fin on the back was missing and his figure is a dorsolateral view instead of a lateral one. These facts explain most of the differences from an accurate sketch of a yellowfin, which include the shorter pectoral fin, shorter anal

TABLE 16.—*Comparison of body proportions calculated from Sloane's figure of Albacore, yellowfin from Angola, Africa, and bluefin tuna from Cape Cod, Mass.*

[Expressed as thousands of fork length]

Character	Sloane's figure [1]	Yellowfin [2]	Atlantic bluefin [3]
	cm.	*cm.*	*cm.*
Fork length	152	140	125.7–131.4
Head length	212	258	284–294
Length of pectoral fin	135	256	197–216
Height of second dorsal fin	270	249	132–145
Height of anal fin	197	268	129–144
Snout to insertion of—			
First dorsal fin	190	280	306–318
Second dorsal fin	489	509	541–559
Anal fin	580	559	606–621
Ventral fins	276	286	315–339

[1] From Sloane (1707) fig. 1, table 1.

[2] From Schaefer and Walford (1950), using the regressions for our large size group and assuming a fork length of 140 cm.

[3] From Godsil and Holmberg (1950), page 7, converted from their ratios of part size to body length.

fin, more slender body, and first dorsal fin too far forward.

Therefore, I concur with Ginsburg and conclude that *T. albacares* (Bonnaterre) 1788 is a valid name for yellowfin tuna. It has priority and hence the appropriate name for a single worldwide species of yellowfin tuna is *Thunnus albacares* (Bonnaterre) 1788.

SUMMARY AND CONCLUSIONS

The study was undertaken in order to understand better the intermingling of the populations of yellowfin tuna and to distinguish the species.

Twenty-four samples of yellowfin tuna from the Pacific Ocean, one from the Atlantic off Angola, Africa, and one from the Indian off Somaliland are compared.

Regression statistics are used to control effect of size of fish in order to compare samples by each of ten characters. Seven of the characters are further used in a multiple character measure of overlap.

The regression equations used by Schaefer (1948) are used. These require log of fork length with log height of second dorsal fin and log height of anal fin, and log fork length with length of pectoral fin. All other characters approximate a linear relationship.

Neither linear, transformed linear, nor simple curvilinear regression equations are completely satisfactory for the full range of the data. Therefore, samples are divided into small fish, less than 80 cm.; medium, 80 to 120 cm.; and large, more than 120 cm. in fork length. Comparisons are made at 65 cm., 100 cm., and 140 cm., respectively.

A cline, or character gradient, exists along the Pacific Equator from the eastern Pacific to the Caroline Islands. The yellowfin in the eastern Pacific have larger heads, slightly shorter pectoral fins, much shorter second dorsal and anal fins, and greater distances from snout to the insertion of first dorsal, second dorsal, ventral, and anal fins. They also have a greater body depth and a greater distance from the insertion of the ventral fins to the vent.

Most other samples were like some part of the cline. The sample from Angola, Africa, closely resembled the samples taken between Costa Rica and the Line Islands. The samples from Hawaii were quite like those taken between longitude 129° W. and the Line Islands. The sample from Japan was like the one from the Caroline Islands. The Bikini Island sample, however, was rather unlike the others but most similar to those from Japan and Hawaii. The Philippine sample was most like samples from the eastern Pacific and very different from the nearby Caroline Islands samples. Most diverse was the sample from Somaliland, which had especially short fins, deep body, and a long distance from the snout to the insertion of the ventrals.

The overlap of samples from along the Pacific Equator is inversely related to distance between samples. The average between samples taken 1,500 miles apart is less than 50 percent; 3,000 miles apart, less than 25 percent; and 6,000 miles apart, less than 6 percent. It is concluded that east-west migration is limited and that most yellowfin remain within a few hundred miles of where they occur as juveniles.

The multivariate analysis is evaluated. It is shown that overlap is greatly reduced by considering more than one character but that it is not worthwhile to use more than four characters.

The distribution of the yellowfin indicates that it belongs to the pelagic faunal group and not to coastal faunal groups. It occurs in all oceans, except the Mediterranean, in waters warmer than 65° F. at the surface. No temperature barrier to movement of the yellowfin exists between the Atlantic and Indian or Indian and Pacific Oceans. The distribution is probably continuous although not uniform.

It is considered desirable to place all yellowfin tunas of the world in a single species because of the continuous distribution and because the full range of characters which have been used to distinguish species occurs in the series of samples from the Pacific Equator. The name should then be *Thunnus albacares* (Bonnaterre) 1788.

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My debt to the many people who have carefully measured thousands of tuna is detailed in a previous paper (Dung and Royce, 1953). The formidable task of analyzing the data has been accomplished almost entirely by Mrs. Dorothy D. Stewart, nee Dung. Joseph J. Graham, Garth I. Murphy, O. E. Sette, and A. L. Tester critically reviewed the manuscript.

LITERATURE CITED

Blunt, C. E., Jr.

1954. Two mid-Pacific recoveries of California-tagged albacore. California Fish and Game, vol. 40, No. 3, p. 339.

Bonnaterre, Joseph P.

1788. Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature . . . Ichthyologie. . . . Published in Paris, by Panckoucke, 1788. 215 pp., 102 plates.

Dung, Dorothy I. Y., and William F. Royce.

1953. Morphometric measurements of Pacific scombrids. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 95, pp. 1–170.

Fraser-Brunner, A.

1950. The fishes of the family Scombridae. The Annals and Magazine of Natural History, vol. 3, No. 26, Series 12, pp., 131–163.

Gansslé, David, and H. B. Clemens.

1953. California-tagged albacore recovered off Japan. California Fish and Game, vol. 39, No. 4, p. 443.

Ginsburg, Isaac.

1953. The taxonomic status and nomenclature of some Atlantic and Pacific populations of yellowfin and bluefin tunas. Copeia, 1953, No. 1, pp. 1–10.

Godsil, H. C.

1948. A preliminary population study of the yellowfin tuna and the albacore. California Department of Natural Resources, Division of Fish and Game, Bureau of Marine Fisheries, Fish Bulletin No. 70, 90 pp.

1954. A descriptive study of certain tuna-like fishes. California Department of Natural Resources, Division of Fish and Game, Bureau of Marine Fisheries, Fish Bulletin No. 97, 185 pp.

Godsil, H. C., and E. C. Greenhood.

1951. A comparison of the populations of yellowfin tuna, *Neothunnus macropterus*, from the eastern and central Pacific. California Department of Natural Resources, Division of Fish and Game, Bureau of Marine Fisheries, Fish Bulletin No. 82, 33 pp.

Godsil, H. C., and Edwin K. Holmberg.

1950. A comparison of the bluefin tunas, genus *Thunnus*, from New England, Australia, and California. California Department of Natural Resources, Division of Fish and Game, Bureau of Marine Fisheries, Fish Bulletin No. 77, 55 pp.

Hubbs, Carl L., and Clark Hubbs.

1953. An improved graphical analysis and comparison of samples. Systematic Zoology, vol. 2, No. 2, pp. 49–56, 92.

Hutchins, L. W., and Margaret Scharff.

1947. Maximum and minimum monthly means sea surface temperatures charted from the "World Atlas of Sea Surface Temperatures." Journal of Marine Research, vol. 6, No. 3, pp. 264–268.

Iversen, Edwin S., and Howard O. Yoshida.

1957. Longline and troll fishing for tuna in the central equatorial Pacific, January 1955 to February 1956. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 203, 38 pp.

LeGall, Jean.

1951. Ichthyométrie des thonidés. De l'emploi d'une technique internationale. Journal du Conseil, vol. 17, No. 3, pp. 267–273.

Mahalanobis, P. C.

1936. On the generalized distance in statistics. Proceedings of the National Institute of Sciences (India), vol. 2, No. 1, pp. 49–55.

Mahalanobis, P. C., R. C. Bose, and S. N. Roy.

1937. Normalization of statistical variates and the use of rectangular coordinates in the theory of sampling distributions. Appendix, Sankhyā, vol. 3, p. 35.

Mahalanobis, P. C., D. N. Majumdar, and C. R. Rao.

1949. Anthropometric survey of the United Provinces, 1941: a statistical study. Sankhyā, vol. 9, nos. 2, 3, pp. 89–266+.

Marr, John C., and Milner B. Schaefer.

1949. Definitions of body dimensions used in describing tunas. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 51, No. 47, pp. 241–244.

Mather, Frank J., III, and C. G. Day.

1954. Observations of pelagic fishes of the tropical Atlantic. Copeia, 1954, No. 3, pp. 179–188.

Mayr, Ernst, E. G. Linsley, and R. L. Usinger.

1953. Methods and principles of systematic zoology. McGraw-Hill, New York. 328 pp.

Murphy, Garth I., and Keith C. Elliott.

1954. Variability of longline catches of yellowfin tuna. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 119, pp. 1–30, March.

Murphy, Garth I., and Richard S. Shomura.

1953a. Longline fishing for deep-swimming tunas in the central Pacific, 1950–51. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 98, 47 pp.

1953b. Longline fishing for deep-swimming tunas in the central Pacific, January–June 1952. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 108, 32 pp.

1955. Longline fishing for deep-swimming tunas in the central Pacific, August–November 1952. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 137, 42 pp.

Pearson, Karl.

1948. Tables for statisticians and biometricians. 3rd ed. Cambridge University Press. 143 pp.

Rao, C. R.

1947. The problem of classification and distance between two populations. Nature, vol. 159, No. 4027, pp. 30–31.

1952. Advanced statistical methods in biometric research. Wiley, New York. 390 pp.

Rivas, Luis Rene.

1954. A preliminary report on the spawning of the western North Atlantic bluefin tuna (*Thunnus thynnus*) in the Straits of Florida. Bulletin of Marine Science of the Gulf and Caribbean, vol. 4, No. 4, pp. 302–322.

Rivas, Luis Rene—Continued

1961. A review of the tuna fishes of the subgenera *Parathunnus* and *Neothunnus* (genus *Thunnus*). Annali del Museo Civico di storia Naturale di Genova, vol. 72, pp. 126-148.

Rosa, Horacio, Jr.

1950. Scientific and common names applied to tunas, mackerels and spearfishes of the world with notes on their geographic distribution. Food and Agriculture Organization of the United Nations, Washington. 235 pp.

Royce, William F.

1953. Preliminary report on a comparison of the stocks of yellowfin tuna. Proceedings Indo-Pacific Fisheries Council, vol. 4 (Section II), pp. 130–145.

1957. Contributions to the study of subpopulations of fishes (co-ordinated by J. C. Marr). [Statistical comparison of morphological data.] U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 208, pp. 7-28.

Schaefer, Milner B.

1948. Morphometric characteristics and relative growth of yellowfin tunas (*Neothunnus macropterus*) from Central America. Pacific Science, vol. 2, No. 2, pp. 114–120.

1952. Comparison of yellowfin tuna of Hawaiian waters and of the American west coast. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 52, No. 72, pp. 353–373.

1955. Morphometric comparison of yellowfin tuna from southeast Polynesia, Central America, and Hawaii. Inter-American Tropical Tuna Commission, Bulletin, vol. 1, No. 4, pp. 91–136.

Schaefer, Milner B., and Lionel A. Walford.

1950. Biometric comparison between yellowfin tunas, (*Neothunnus*) of Angola and of the Pacific coast of Central America. U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 51, No. 56, pp. 425–443.

Sette, Oscar E., and POFI.

1954. Progress in Pacific Oceanic Fishery Investigations 1950–53. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 116, 75 pp.

Shomura, Richard S., and Garth I. Murphy.

1955. Longline fishing for deep-swimming tunas in the central Pacific, 1953. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 157, 70 pp.

Sloane, Hans.

1707. A voyage to the islands Madera, Barbados, Nieves, S. Christophers and Jamaica with the natural history of the herbs and trees, four footed beasts, fishes, birds, insects, reptiles, etc., of the last of those islands. Vol. I. Printed by B. M. for the author. London, 1707. 16 folio plates, CLIV, 264 pp.

Tsuruta, Saburo.

1954. Morphometric comparison of yellowfin tuna of southwestern Pacific, off southwest of Gilbert Islands and of Hawaiian waters. Journal of the Shimonoseki College of Fisheries, vol. 3, No. 3, pp. 217-228.

Wilson, Robert C.

1953. Tuna marking, a progress report. California Fish and Game, vol. 39, No. 4, pp. 429–442.

APPENDIX

Table A-1.—*Morphometric measurements of yellowfin tuna (mm.), from longline catches near the Equator and longitude 110° W., March 1954*

Fork length	Weight (lb.)	Head length	Snout to insertion of—				Insertion of ventral fin to anterior edge of vent	Greatest body depth	Length of pectoral fin	Height of—		Diameter of iris	Sex	Examiner
			First dorsal fin	Second dorsal fin	Anal fin	Ventral fin				Second dorsal fin	Anal fin			
764	--------	217	243	416	454	238	----------	188	207	98	99	33	F	William F. Royce.
800	23¼	223	242	430	479	243	242	214	225	113	113	30	M	Do.
823	--------	228	247	435	487	252	235	202	242	119	119	31	F	Do.
1051	--------	288	310	552	605	319	----------	278	284	180	186	38	M	Do.
1175	--------	310	342	616	678	350	343	306	309	222	205	36	F	Do.
1180	--------	309	334	605	678	333	----------	300	310	229	246	40	F	Do.
1206	--------	308	341	627	689	344	353	293	322	218	213	34	F	Do.
1232	--------	314	339	623	692	353	346	303	308	216	234	35	F	Do.
1283	--------	325	359	661	733	365	377	311	330	276	269	36	F	Do.
1412	--------	350	387	722	791	391	----------	348	336	363	434	40	F	H. S. H. Yuen.
1446	--------	367	417	735	819	411	----------	375	341	368	465	41	M	Do.
1449	--------	360	400	732	816	399	428	380	356	378	416	41	M	William F. Royce.
1465	--------	367	394	779	819	404	421	362	380	396	381	44	F	Do.
1466	--------	366	383	737	817	400	448	388	343	366	319	38	M	Do.
1476	--------	379	416	765	844	420	441	391	369	379	404	40	F	H. S. H. Yuen.
1480	--------	369	391	756	840	419	427	379	358	363	393	38	F	Do.
1507	--------	388	417	767	851	431	445	382	347	362	443	42	F	Do.
1525	--------	385	425	764	853	430	433	398	378	391	465	40	M	Do.
1531	--------	404	445	781	858	454	----------	417	371	446	512	42	M	Do.
1537	--------	379	420	777	846	417	----------	400	379	417	434	45	M	William F. Royce.
1567	165	387	429	791	880	428	461	411	[1]361	--------	592	42	F	H. S. H. Yuen.
1603	--------	408	437	813	893	459	452	420	367	506	[1]0	41	M	Do.
608	--------	408	430	803	913	466	457	417	358	458	543	40	M	Do.
649	--------	415	450	828	906	454	470	429	391	420	502	41	M	Do.
650	--------	435	457	828	908	472	453	427	375	477	362	40	M	Do.
680	200	429	438	841	937	471	478	445	404	493	543	42	M	W. F. Royce.
690	220	427	483	871	957	471	508	454	406	640	716	46	M	Do.

[1] Frayed.

TABLE A-2.—*Morphometric measurements (cm.) of yellowfin tuna taken near Bender Cassim, Somaliland, Africa*

[Measured by A. Fraser-Brunner]

Fork length	Weight (kg.)	Head length	Snout to insertion of—				Insertion of ventral fin to anterior edge of vent	Greatest body depth	Length of pectoral fin	Height of—		Diameter of iris	Number of gill rakers	Sex	Months of 1953
			First dorsal fin	Second dorsal fin	Anal fin	Ventral fin				Second dorsal fin	Anal fin				
62.5	5.25	18.5	20.5	34	39	23	----------	16.5	16.5	7	6.5	2.5	9+18	M	March.
65	6.3	18.75	20	35.5	40	21.5	----------	17	18	7.25	7.5	3	8+20	M	February.
65	6.4	19	21	36	40	21.5	----------	17	18	8.5	8	3.5	9+18	F	January.
65	6.4	19	21.5	36.5	39.5	21	----------	17	17.5	9	9	3.5	9+18	F	February.
67.5	6	19.5	22.5	37.5	42	22	----------	17	18.5	8.5	9	3	10+19	F	Do.
68	6	19.5	23	38	42	22	----------	17.5	18.5	8.5	9	3	10+19	F	January.
69.5	6.4	20	21.5	38	42	22	----------	18.5	19	9.5	10	3.25	10+21	M	February.
70	5.6	20	24	41	44	23	----------	20	19.5	8.5	8	3	8+20	M	January.
70	5.8	20	22	29	43	22	----------	17.5	18	8.5	8	3.5	10+18	F	March.
70	7	20	22	29	43	22	----------	17.5	18	8	8.8	3.5	9+19	F	Do.
70.5	5	20	23	39	42.5	23	----------	18.5	19	8.5	8	3	9+20	F	January.
70.5	5.4	20.5	22	38	42.5	23.5	----------	18.5	18.5	8.5	8	3	9+20	M	February.
70.5	5.8	20	23.5	39	43	23	----------	19	20	9	8	3.5	9+20	F	January.
71.5	7.8	20.5	22.5	39	43	23.5	----------	19	18.5	8.25	9	3.5	9+20	F	March.
72	7	20.5	22.5	39.5	43	23	----------	19	20	8	8.5	3.5	10+20	M	Do.
73	8	20.5	22.5	38	45	24	----------	19	19.5	10	10	3.25	9+20	M	Do.
73	8	20.5	22	37.5	45	24	----------	19	19.5	9.5	10	3.5	9+20	M	Do.
73.5	7.3	20.5	23	39	44	23.5	----------	19	19.5	8.5	8.5	3	9+20	F	Do.
74	8	21	25	42	45	24	----------	20	20	9	11	3.5	9+20	F ?	February.
74	8	21	24	41	45.5	25	----------	20	20	9	10	3.5	9+20	M	March.
75	7.7	21.5	23	41.5	46	24	----------	19.5	20	9.5	10	3.5	9+19	F	Do.
76	5.5	18.5	21	36	40	21	----------	16.5	19	8	8.25	3.5	9+21	M	Do.
76	6	18.5	21	35	40	21.5	----------	16.5	13	8.5	8.25	3.5	9+21	M	Do.
76	9	22	24.5	42	46	25	----------	20.5	21.5	10	11.5	3.5	9+22	F	Do.
77	5.5	19	21.5	36.5	40.5	22	----------	17	19	8	8.5	3.5	9+20	M	Do.
80	10	23	24	42.5	49.5	26	----------	22	20	11.25	12	3.5	9+20	F	Do.
80	10	23	24	42.5	49	25	----------	22	20	11	11.5	3.75	10+20	F	Do.
80	11	23	26	44	48.5	26	----------	22	21.5	11	12	4	9+20	F	Do.
80	11	23	26	44	48	26	----------	22	21.5	11	12	4	9+21	F	Do.
80.5	10	22.5	25	44	48	26	----------	21	20.5	9.5	10	4	9+21	F	Do.
80.5	10	22.5	25	44	48	26	----------	21	20	9.5	10	4	9+22	F	Do.
81	10	23	25.5	44	47	25.5	----------	21	21	9	11	3.5	8+20	M	Do.
81	10	23	24	43	50	26	----------	22.25	20	11.5	12	3.75	9+20	F	Do.
81	10.7	23	25.5	44	47	25.5	----------	21	21	9	11	3.5	9+20	M	Do.
81.5	10	23	25	43.25	44	27	----------	20.5	22.5	9.5	10	4	10+22	F	Do.
81.5	10	24	26.5	44	49	25	----------	22	20.5	9.5	12	3.5	10+21	F	Do.
82	11.6	24	27	45.5	49	26	----------	21.5	23.5	10.5	12.5	4	10+22	M	Do.
82.5	10.5	22.5	24	43.5	46.5	24	----------	22	22.5	12	14	3.5	9+20	M	Do.
83	11.5	23	25.5	44.5	50	26.5	----------	22	21.5	11	12	3.5	9+20	F	Do.
83	11.7	23.5	25.5	44.5	50.5	26.5	----------	21.5	21.5	11	11.5	3.5	9+20	F	Do.
84	11	22.5	26	45	50	26.5	----------	22.5	22	11	13	3.5	9+20	F	Do.
84	11.8	23.5	25.5	44.5	50.5	26.5	----------	21.5	21.5	11	11	3.5	10+20	F	Do.
84	12	24	26.5	45	50	27	----------	23	21	11	12	4	10+20	M	Do.
84	12	24.5	26	46	50	27	----------	22.5	21	10.5	11.5	4	9+20	M	Do.
84	12.6	24	27	45	50.5	27	----------	22.5	21	11	12.5	4.25	9+21	M	Do.
84.5	12	24.5	26	47	52	28.5	----------	23	23	12.5	16.5	3.5	8+20	F	Do.
84.5	12	23	26	45.5	50.5	26.5	----------	22	21.5	11.5	11.5	4	9+21	M	Do.
84.5	12.7	23	26	45.5	50.5	26.5	----------	22	23	11.5	11.5	4	8+21	M	Do.
85.5	12	23.5	26.5	45	51	26	----------	22.5	22	11	14	4	10+20	F	Do.
86	12	23.5	27	45	49	26	----------	23	22	11.5	10.5	4	8+21	F	Do.
86	13	24	27.5	46.5	52.5	27.5	----------	23	24	12 5.	14	3.5	9+20	M	Do.
86	13	24	27	46.5	51	27.5	----------	23	22	12	13	4	10+20	F	Do.
87	13	24.5	26.5	45.5	50.5	26.5	----------	23.5	22	12	12	4	9+22	F	Do.
87	13.3	24.5	27	46	52	27.5	----------	23	24.5	13	14.5	3.75	9+20	M	Do.
89	14	26	28	48	52	29	----------	24	23	13.5	15	4	8+20	F	Do.
105.5	22	28	31.5	56	61	31.5	----------	27	26	16	18	4	9+20	M	Do.

NOTE.—Data furnished through the courtesy of G. L. Kesteven, Fisheries Division, U.N. Food and Agriculture Organization. Measurements were recorded in half or quarter centimeter units identified by the upper limit of each unit; thus are ⅛ to ¼ cm. too great.

TABLE A-3.—*Regression statistics of yellowfin tuna samples*

[N=number used in sample; S=summation; X=fork length (mm.) or log. (mm.); Y=other characters as listed; x=deviations from mean $\bar{x}$; y=deviation from mean $\bar{y}$; b=regression coefficient; a=constant in regression equation; s=standard deviation from regression (cm.); $\hat{Y}$=estimated character size (cm.) at standard comparison length of size group (cm. except for logarithms which have characteristics for mm.)]

Character and size group [1]	N	SX	SY	SX^2	SY^2	SXY	Sx^2
X=fork length; Y=head length:							
Costa Rica:[2] *M*	29	2,896.5	789.9	292,493.79	21,688.87	79,625.98	3,193.3676
109°–119° W.: *L*	21	3,146.2	797.0	475,009.34	30,504.64	120,353.68	3,648.6524
119°—129° W.: *L*	47	6,895.9	1,739.1	1,016,781.01	64,638.71	256,300.39	5,005.7588
129°–139° W.: *L*	46	6,667.6	1,680.6	988.059.18	62,520.78	248,469.53	21,605.0548
139°–149° W.: *L*	111	16,507.1	4,150.5	2,468,765.29	156,032.57	620,546.47	13,951.3223
East Line Islands:							
M	33	3,382.8	913.8	349,710.50	25,445.64	94,305.02	2,942.7473
L	155	22,524.5	5,631.8	3,288,056.75	205,463.66	821,786.66	14,810.9420
West Line Islands:							
S	43	2,954.4	849.3	205,448.86	16,939.55	58,973.52	2,460.9680
M	86	8,407.2	2,286.3	832,615.32	61,334.71	225,881.39	10,743.0894
L	57	7,876.2	1,998.8	1,094,133.62	70,433.44	277,547.24	5,808.5948
Palmyra Island:[3]							
S	35	2,537.2	730.7	184,770.90	15,308.81	53,170.94	845.6475
M	57	5,379.7	1,446.6	511,367.03	36,886.28	137,303.18	3,627.1688
Phoenix Islands:							
S	37	2,503.6	715.2	171,117.96	13,927.34	48,798.54	1,712.2044
M	59	5,795.3	1,559.6	576,982.99	41,586.04	154,811.32	7,737.1918
L	46	6,142.5	1,539.6	836,866.39	52,633.16	209,836.18	16,642.3411
East Marshall Islands: *L*	40	5,453.4	1,359.8	746,253.02	46,398.12	186,058.56	2,763.7310
Bikini Island: *S*	31	1,829.9	520.9	109,843.77	8,859.57	31,185.95	1,826.5439
East Caroline Islands:							
S	60	3,916.3	1,096.1	259.183.29	20,224.83	72,382.71	3,559.8619
M	55	5,404.4	1,411.5	539,532.20	36.602.69	140,475.74	8,486.0298
L	54	7,516.0	1,872.4	1,052,115.44	65,213.40	261,891.54	5,999.5882
Central Caroline Islands:							
S	37	2,513.9	698.9	173,346.55	13,369.39	48,132.23	2,544.0309
M	102	10,289.2	2,673.5	1,049,698.10	70,639.51	272,240.75	11,780.0938
L	69	9,125.8	2,287.5	1,211,069.54	76,126.13	303,577.84	4,109.7482
Philippines (SW. Panay):							
S	242	15,776.4	4,550.2	1,040,719.56	86,405.94	299,786.77	12,228.6635
M	81	7,349.8	1,993.6	674,621.22	49,439.00	182,526.67	7,713.0714
L	32	4,234.2	1,085.1	562,353.60	36,933.97	144,065.00	2,089.5488
Japan: *S*	31	1,789.5	508.7	108,296.33	8,686.13	30,660.85	4,995.9994
Hawaii:[2]							
S	36	1,884.6	534.2	100,518.50	8,061.62	28,461.45	1,859.6900
M	34	3,466.4	913.2	356,040.12	24,662.30	93,673.95	2,630.4448
L	133	19,955.4	4,929.5	3,028,042.30	184,479.19	747,259.96	33,922.0808
Hawaii:[3]							
S	47	2,679.3	762.9	153,111.13	12,412.53	43,589.67	373.9281
L	20	2,859.2	714.2	409,803.42	25,588.64	102,393.11	1,052.1880
Society Islands: *S*	17	988.5	284.4	58,503.31	4,827.06	16,801.56	1,024.9424
Northeast Africa: *S*	48	3,805.0	1,077.3	304,447.00	24,356.69	86,085.00	2,821.4792
Angola, Africa:[4]							
M	21	2,050.5	560.5	206,277.69	15,248.01	56,039.06	6,061.0115
L	27	3,717.0	961.3	515,125.62	34,411.43	133,110.49	3,418.6200
Y=pectoral fin length:							
Costa Rica:[2] *M*	28	83.897	755.5	251.444377	20,519.41	2,266.4008	.061998
109°–119° W.: *L*	21	66.650	758.0	211.566268	27,490.42	2,407.5195	.031863
119°–129° W.: *L*	46	154.626	1.680.7	461.064214	61,652.59	5,322.9928	.043956
129°–139° W.: *L*	46	145.115	1,650.4	458.098769	60,123.18	5,222.2868	.308265
139°–149° W.: *L*	113	358.339	4,216.1	1,136.467083	157,636.55	13,374.0386	.123376
East Line Islands:							
L	124	391.907	4,570.7	1,238.755335	168,894.65	14,450.0028	.117459
M	32	96.266	917.8	289.652924	26,501.70	2,763.9444	.054713
West Line Islands:							
S	43	121.882	874.9	345.577724	18,022.45	2,484.4753	.107447
M	86	256.925	2,418.1	767.775975	68,804.05	7,236.1381	.212538
L	56	175.831	2,030.0	552.137153	73,803.70	6,376.8446	.056072
Phoenix Islands:							
S	37	104.643	751.9	296.022337	15,457.43	2,129.8423	.072136
M	58	173.291	1,696.1	517.898774	50,125.13	5.075.4469	.144108
L	46	143.943	1,643.0	450.460353	58,862.76	5,142.9820	.034544
East Marshall Islands: *L*	40	125.349	1,441.5	392.839243	52,058.77	4,518.3636	.029948
Bikini Island: *S*	31	85.798	558.8	237.546178	10,226.10	1,550.0649	.084991
East Caroline Islands:							
S	60	168.697	1,239.1	474.472711	25,954.71	3,491.1148	.161415
M	53	158.390	1,568.3	473.500596	46,927.19	4,695.2196	.153576
L	53	173.007	2,023.5	544.271157	74,624.13	6,367.6164	.063484
Central Caroline Islands:							
S	36	101.854	778.3	288.288240	17,128.15	2,207.7750	.114982
M	102	306.117	3,125.4	918.930769	96,471.08	9,391.1201	.228635
L	72	224.688	2,576.1	701.222332	92,354.33	8,040.8810	.054980
Japan: *S*	30	82.441	515.3	226.832298	9,385.21	1,428.2000	.281682
Hawaii:[2]							
S	36	97.754	550.6	265.544952	8,636.70	1,499.6342	.104827
M	34	102.230	990.4	307.429448	29,046.90	2,980.3779	.047893
L	133	422.105	5,032.9	1,339.929970	191,379.69	15,986.6720	.286128
Society Islands: *S*	21	57.897	374.4	159.676581	6,854.34	1,035.2576	.054552
Northeast Africa: *S*	48	139.053	999.5	402.913285	20,984.25	289.8690	.085435
Angola, Africa:[4]							
M	21	62.646	569.8	187.000176	15,924.06	1,707.0178	.118209
L	27	84.710	953.7	265.799772	33,830.51	2,993.9101	.029991

See footnotes at end of table.

Character and size group [1]	*N*	*SX*	*SY*	SX^2	SY^2	*SXY*	Sx^2
Y=height second dorsal fin:							
Costa Rica: [2] *M*	28	83.896	61.318	251.435890	134.538996	183.841218	0.059504
109°–119° W.: *L*	20	63.455	51.701	201.358243	133.893361	164.117955	.031392
119°–129° W.: *L*	45	142.407	116.934	450.704783	304.507574	370.192937	.043591
129°–139° W.: *L*	45	141.932	115.801	447.967280	299.620879	365.902722	.307444
139°–149° W.: *L*	109	345.664	287.463	1,096.300848	759.324805	911.908839	.121023
East Line Islands:							
M	32	96.220	72.790	289.372416	165.827650	218.957612	.050903
L	155	489.958	412.957	1,548.906650	1,102.197991	1,305.785473	.139929
West Line Islands:							
S	42	119.137	83.006	338.044643	164.358096	235.620544	.101197
M	84	250.789	189.036	748.954439	426.449708	564.797120	.202981
L	57	178.935	149.275	561.771969	391.669033	468.777214	.057334
Phoenix Islands:							
S	36	101.821	71.606	288.058653	142.698836	202.657672	.072097
M	55	164.262	125.241	490.710168	285.685185	374.264864	.128266
L	44	137.612	114.589	430.427680	298.849489	358.489012	.039895
East Marshall Islands: *L*	38	119.107	100.708	373.357959	267.224844	315.739082	.029606
Bikini Island: *S*	30	82.938	55.723	229.368553	103.721167	154.177996	.078158
East Caroline Islands:							
S	60	168.697	118.869	474.472711	235.963849	334.477887	.161415
M	55	164.390	126.919	491.509308	293.653623	379.691955	.162543
L	54	169.785	144.748	533.898401	388.441770	455.251731	.066064
Central Caroline Islands:							
S	36	101.779	72.384	287.862165	145.852994	204.828458	.113142
M	102	306.117	237.642	918.930769	554.766056	713.671426	.228635
L	71	221.566	185.713	691.475448	486.391527	579.669959	.045979
Japan: *S*	31	85.269	57.732	234.830567	108.176324	159.229245	.288555
Hawaii: [2]							
S	33	89.605	59.351	243.40909	106.99218	161.30666	.10436
M	34	102.231	77.106	307.43281	175.05126	231.91726	.04524
L	133	422.105	352.442	1,339.93162	936.08809	1,119.25091	.28778
Society Islands: *S*	20	55.062	37.280	151.647056	69.692726	102.737708	.055864
Northeast Africa: *S*	43	124.960	86.819	363.189526	175.472595	252.384244	.049954
Angola, Africa: [4]							
M	20	59.739	44.580	178.549527	99.720328	133.352250	.112121
L	26	81.631	65.771	256.319531	166.546780	206.553552	.06448
Y=height anal fin:							
Costa Rica: [2] *M*	28	83.898	62.249	251.448856	138.676825	186.641229	.060484
109°–119° W.: *L*	20	63.445	52.351	201.294243	137.360109	166.158030	.030842
119°–129° W.: *L*	46	145.618	121.359	461.013894	320.731273	384.301592	.044287
129°–139° W.: *L*	44	138.731	115.337	437.720969	304.022121	364.330992	.305279
139°–149° W.: *L*	110	348.752	295.097	1,105.828784	792.763031	935.861205	.120079
East Line Islands:							
M	33	99.292	76.066	298.809600	175.647828	228.981829	.055016
L	153	483.531	414.601	1,528.254051	1,125.407081	1,310.662739	.134914
West Line Islands:							
S	42	119.118	83.219	337.939288	165.233633	236.198792	.103624
M	87	259.891	199.596	776.573131	459.480550	596.750578	.212995
L	54	169.496	144.323	532.067676	386.427807	453.165245	.051121
Phoenix Islands:							
S	37	104.641	73.489	296.010719	146.301409	207.982031	.071831
M	58	173.326	134.937	518.112303	314.633461	403.515203	.148471
L	43	134.444	114.370	420.379512	304.506932	357.661681	.026277
East Marshall Islands: *L*	39	122.276	105.833	383.395914	287.459047	331.880495	.026166
Bikini Island: *S*	31	85.907	57.758	238.182920	108.065174	160.283217	.117996
East Caroline Islands:							
S	60	168.697	119.181	474.472711	237.383145	335.404648	.161415
M	55	164.390	129.428	491.509308	305.394016	387.198621	.162543
L	52	163.420	142.437	513.642164	390.578717	447.776963	.063388
Central Caroline Islands:							
S	35	99.042	70.543	280.380896	142.657533	199.846930	.114674
M	101	303.205	239.524	910.451025	569.235948	719.542609	.220609
L	70	218.412	187.800	681.527732	504.318644	586.077836	.044850
Japan: *S*	30	82.632	55.604	227.876798	103.864654	153.619860	.275217
Hawaii: [2]							
S	34	92.360	60.270	250.99237	107.19607	163.90159	.09915
L	133	422.105	358.549	1,339.93164	968.75793	1,138.64039	.28780
M	34	102.239	78.230	307.48041	180.25731	235.32153	.04473
Society Islands: *S*	19	52.360	35.319	144.346252	65.858589	97.429882	.053115
Northeast Africa: *S*	43	124.960	88.273	363.189526	181.467413	256.620348	.049954
Angola, Africa: [4]							
M	21	62.646	46.863	187.000176	105.043883	140.028416	.118209
L	27	84.710	69.103	265.801668	177.057928	216.862426	.031887
Y=snout to insertion first dorsal fin:							
Costa Rica: [2] *M*	29	2,896.5	853.9	292,493.79	25,390.27	86,162.62	3,193.3676
109°–119° W.: *L*	21	3,146.2	865.8	475,009.34	35,969.34	130,656.84	3,648.6524
119°–129° W.: *L*	44	6,450.3	1,784.5	950,350.67	72,671.25	262,735.30	4,751.3498
129°–139° W.: *L*	46	6,667.6	1,848.3	988,059.18	75,600.75	273,216.64	21,605.0548
139°–149° W.: *L*	112	16,645.1	4,573.0	2,487,698.53	187,782.94	683,312.55	13,954.2978
East Line Islands:							
M	33	3,382.8	981.3	349,710.50	29,370.83	101,318.62	2,942.7473
L	155	22,538.9	6,152.4	3,292,495.07	245,222.02	898,248.44	15,062.7267
West Line Islands:							
S	44	3,022.1	935.9	210,032.15	20,100.84	64,948.35	2,461.9589
M	86	8,402.3	2,459.2	831,632.87	70,984.24	242,859.66	10,718.3899
L	55	7,576.8	2,068.7	1,049,124.22	78,177.79	286,342.03	5,344.2520
Palmyra Island: [3]							
S	35	2,537.2	797.5	184,770.90	18,240.39	58,031.19	845.6475
M	57	5,379.7	1,586.9	511,367.03	44,399.43	150,634.50	3,627.1688
Phoenix Islands:							
S	35	2,384.8	740.5	164,052.42	15,795.21	50,893.93	1,558.9618
M	59	5,795.3	1,690.9	576,982.99	48,913.93	167,924.19	7,737.1919
L	45	6,069.5	1,670.0	822,105.79	62,171.48	22,601.378	3,465.1178

See footnotes at end of table.

TABLE A-3.—*Regression statistics of yellowfin tuna samples*—Continued

Character and size group [1]	*N*	*SX*	*SY*	*SX* [2]	*SY* [2]	*SXY*	*Sx* [2]
East Marshall Islands: *L*	39	5,310.9	1,461.4	725,946.77	54,957.40	199,720.51	2,724.7493
Bikini Island: *S*	31	1,829.9	560.6	109,843.77	10,254.82	33,547.13	1,826.5439
East Caroline Islands:							
S	59	3,861.4	1,189.4	256,169.28	24,203.44	78,707.02	3,450.4672
M	55	5,404.4	1,560.8	539,532.20	44,782.08	155,380.26	8,486.0298
L	56	7,837.2	2,150.0	1,103,798.16	83,008.82	302,614.71	6,982.0200
Central Caroline Islands:							
S	35	2,378.7	729.8	163,986.53	15,390.80	50,225.33	2,323.2818
M	102	10,289.2	2,955.1	1,049,698.10	86,320.21	300,905.71	11,780.0938
L	71	9,404.3	2,597.7	1,249,939.11	95,321.55	345,077.67	4,293.2158
Philippines (SW. Panay):							
S	242	15,776.4	5,121.5	1,040,719.56	109,406.73	337,258.66	12,228.6635
M	81	7,349.8	2,232.5	674,621.22	61,959.87	204,321.76	7,713.0714
L	33	4,388.7	1,243.0	586,223.85	47,014.72	165,933.26	2,566.6473
Japan: *S*	31	1,789.5	564.0	108,296.33	10,681.40	33,999.64	4,995.9994
Hawaii: [2]							
S	36	1,884.6	601.8	100,518.50	10,234.96	32,067.13	1,859.6900
M	34	3,466.4	1,015.2	356,040.12	30,484.58	104,134.53	2,630.4448
L	131	19,610.4	5,379.7	2,968,469.30	222,997.89	813,401.91	32,837.3299
Hawaii: [3]							
S	47	2,679.3	834.6	153,111.13	14,856.44	47,686.86	373.9281
L	20	2,859.2	794.0	409,803.42	31,624.14	113,819.11	1,052.1880
Society Islands: *S*	22	1,260.6	400.2	73,377.44	7,375.30	23,254.99	1,145.0600
Northeast Africa: *S*	48	3,805.0	1,189.5	304,447.00	29,713.75	95,067.25	2,821.4792
Angola, Africa: [4]							
M	21	2,050.5	606.8	206,277.69	17,860.48	60,639.16	6,061.0115
L	27	3,717.0	1,042.7	515,125.62	40,514.29	144,427.97	3,418.6200
Y=snout to insertion second dorsal fin:							
Costa Rica: [2] *M*	29	2,896.5	1,527.6	292,493.79	81,184.30	154,073.13	3,193.3676
109°–119° W.: *L*	21	3,146.2	1,600.1	475,009.34	122,765.07	241,457.31	3,648.6524
119°–129° W.: *L*	44	6,470.7	3,255.9	956,166.11	241,933.41	480,926.32	4,576.1444
129°–139° W.: *L*	46	6,667.6	3,364.6	988,059.18	250,829.34	497,756.66	21,605.0548
139°–149° W.: *L*	112	16,666.4	8,371.8	2,494,141.78	629,133.06	1,252,559.93	14,062.4142
East Line Islands:							
M	33	3,382.8	1,739.9	349,710.50	92,411.27	179,750.04	2,942.7473
L	155	22,517.6	11,248.8	3,268,363.68	819,667.82	1,641,017.17	15,142.9719
West Line Islands:							
S	43	2,947.9	1,588.1	204.526.51	59,288.09	110,045.93	2,430.8261
M	86	8,394.8	4,337.7	830,036.12	221,074.05	428,290.45	10,586.5033
L	56	7,732.7	3,868.1	1,073,541.37	268,490.83	536,827.26	5,779.7756
Palmyra Island: [3]							
S	34	2,468.9	1,329.1	180,106.01	52,136.85	96,888.92	827.5627
M	57	5,379.7	2,796.1	511,367.03	137,936.41	265,548.40	3,627.1688
Phoenix Islands:							
S	37	2,503.6	1,347.5	171,117.96	49.464.81	91,972.04	1,712.2044
M	59	5,795.3	2,978.1	576,982.99	151,964.35	295,988.89	7,737.1919
L	46	6,207.1	3,110.9	841.039.55	211,181.35	421,398.64	3,472.3672
East Marshall Islands: *L*	39	5,321.7	2,675.8	728,908.13	184,225.62	366,426.68	2,741.6970
Bikini Island: *S*	31	1,829.9	993.7	109,843.77	32,271.29	59,529.17	1,826.5439
East Caroline Islands:							
S	59	3,844.2	2,063.0	253,984.88	72,921.12	136,067.49	3.512.4455
M	55	5,404.4	2,764.7	539,532.20	140,667.69	275,442.73	8.486.0298
L	56	7,837.2	3,881.4	1,103,798.16	270,556.54	546,441.18	6,982.0200
Central Caroline Islands:							
S	37	2,513.9	1,344.8	173,346.55	49,485.68	92,604.46	2,544.0309
M	101	10,183.7	5,180.5	1,038,567.85	268,193.53	527,681.15	11,758.4870
L	68	8,997.1	4,472.9	1,194,303.33	295,159.21	593,660.04	3,894.3828
Philippines (SW. Panay):							
S	241	15,711.8	8,908.0	1,036,546.40	332,391.36	586.730.54	12,228.3119
M	81	7,349.8	3,996.1	674,621.22	198,764.79	366,077.21	7,713.0714
L	28	3,713.5	1,925.6	494,392.59	132,923.10	256,315.20	1,889.6525
Japan: *S*	31	1,789.5	979.4	108,296.33	32.243.84	59,082.02	4,995.994
Hawaii: [2]							
S	36	1,884.6	1,041.4	100,518.50	30,637.02	55,486.52	1,859.6900
M	34	3,466.4	1,800.3	356,040.12	95,877.41	184,731.92	2,630.4448
L	132	19,777.4	9,852.0	2,996,358.30	742,617.26	1,491,512.29	33.134.4306
Hawaii: [3]							
S	47	2,679.3	1,463.8	153,111.13	45,690.52	83,635.85	373.9281
L	20	2,859.2	1,437.6	409,803.42	103,634.86	206,068.57	1,052.1880
Society Islands: *S*	21	1,209.3	665.7	70,745.75	21.367.69	38,872.54	1,107.3458
Northeast Africa: *S*	46	3,665.0	1,978.2	294,647.00	85.750.74	158,920.80	2,642.1087
Angola, Africa: [4]							
M	21	2,050.5	1,089.0	206,277.69	57,692.46	109,041.36	6,061.0115
L	27	3,717.0	1.892.8	515,125.62	133,489.44	262,208.21	3,418.6200
Y=snout to insertion anal fin:							
Costa Rica: [2] *M*	29	2,896.5	1,709.6	292,493.79	101,685.80	172,442.86	3,193.3676
109°–119° W.: *L*	21	3,146.2	1,766.2	475,009.34	149,575.84	266,533.77	3.648.6524
119°–129° W.: *L*	47	6,895.9	3,825.4	1,016,781.01	312,644.10	563,751.14	5,005.7588
129°–139° W.: *L*	46	6,667.6	3,711.3	988,059.18	305,168.05	549,037.23	21,605.0548
139°–149° W.: *L*	113	16,807.0	9,330.2	2,513,910.14	774,456.74	1,395,190.05	14,129.1754
East Line Islands:							
M	32	3,285.0	1,869.7	340,145.66	110,060.09	193,454.86	2,919.8788
L	153	22,239.8	12,270.3	3,247,595.60	988,185.19	1,791,256.16	14,858.9724
West Line Islands:							
S	43	2,956.6	1,750.1	205,741.90	71,942.63	121,639.51	2,451.5847
M	86	8,405.2	4,786.3	832,220.21	269,255.43	473,284.60	10,738.9654
L	56	7,724.0	4,286.3	1,070,968.78	329,570.95	594,058.99	5,608.4943
Palmyra Island: [3]							
S	35	2.537.0	1,503.1	184.770.90	64,785.69	109,397.75	845.6475
M	57	5,379.7	3,069.5	511,367.03	166,188.61	291,470.97	3,627.1688
Phoenix Islands:							
S	36	2,446.3	1,439.9	167,834.67	58,036.31	98,677.17	1,601.7898
M	58	5,697.8	3,229.9	567,476.74	181,796.19	321,112.35	7,736.6566
L	45	6,078.7	3,350.5	824,552.99	250,453.07	454,396.25	3,428.6858

See footnotes at end of table.

TABLE A-3.—*Regression statistics of yellowfin tuna samples*—Continued

Character and size group [1]	N	SX	SY	SX^2	SY^2	SXY	Sx^2
East Marshall Islands: *L*	40	5,453.4	3,002.7	746,253.02	226,261.25	410,890.35	2,763.7310
Bikini Island: *S*	31	1,829.9	1,094.9	109,843.77	39,177.77	65,588.67	1,826.5439
East Caroline Islands:							
S	60	3,916.3	2,302.4	259,183.29	89,401.86	152,204.64	3,559.8619
M	54	5,312.8	2,982.3	531,141.64	166,751.45	297,557.13	8,440.8282
L	55	7,682.1	4,195.5	1,079,742.15	321,854.99	589,467.25	6,748.3244
Central Caroline Islands:							
S	37	2,513.9	1,489.0	173,346.55	60,687.04	102,546.64	2,544.0309
M	102	10,289.2	5,796.7	1,049,698.10	332,230.77	590,407.37	11,780.0938
L	68	8,977.3	4,940.0	1,189,017.29	360,056.26	654,229.69	3,842.0652
Philippines (SW. Panay):							
S	242	15,776.4	9,798.3	1,040,719.56	400,472.31	645,393.74	12.228.6635
M	81	7,349.8	4,391.4	674,621.22	240,101.84	402,363.09	7,713.0714
L	31	4,109.1	2,351.4	546,703.59	178,857.86	312,602.05	2,035.7575
Japan: *S*	31	1,789.5	1,071.4	108,296.33	38,581.78	64.628.88	4,995.9994
Hawaii: [2]							
S	36	1,884.6	1,144.4	100,518.50	36,977.80	60,956.99	1,859.6900
M	34	3,466.4	1,988.6	356,040,12	117,014.20	204,081.16	2,630.4448
L	132	19,809.0	10,946.0	3,006,609.34	916,354.34	1,659,647.04	33,908.7264
Hawaii: [3]							
S	47	2,679.3	1,613.8	153,111.13	55,536.18	92,207.49	373.9281
L	20	2,859.2	1,599.7	409,803.42	128,289.01	229,277.36	1,052.1880
Northeast Africa: *S*	47	3,723.5	2,236.5	297,804.75	107,216.25	178,643.00	2,816.4043
Angola, Africa: [4]							
M	21	2,050.5	1,196.7	206,277.69	69,706.95	119,863.37	6,061.0115
L	26	3,559.3	1,994.1	490,256.33	153,727.69	274,493.04	3,001.8497
Y=snout to insertion ventral fin:							
109°–119° W.: *L*	21	3,146.2	885.9	475,009.34	37,666.19	133,726.71	3,648.6524
119°–129° W.: *L*	47	6,895.9	1,929.5	1,016,781.01	79,629.77	284,429.37	5,005.7588
129°–139° W.: *L*	46	6,667.6	1,867.5	988,059.18	77,173.33	276,043.66	21,605.0548
139°–149° W.: *L*	113	16,807.0	4,688.3	2,513,910.14	195,546.89	700,965.38	14,129.1754
East Line Islands:							
M	31	3,183.1	955.3	329,762.05	29,610.51	98,779.60	2,919.2884
L	153	22,222.4	6,212.5	3,242,746.86	253,634.17	906,612.53	15,066.7178
West Line Islands:							
S	42	2,889.5	923.4	201,158.85	20,499.36	64,190.27	2,368.1298
M	84	8,216.6	2,495.6	814,259.78	74,868.24	246,773.28	10,539.3567
L	56	7,735.2	2,217.1	1,074,252.62	88,196.69	307,744.22	5,800.4943
Palmyra Island: [3]							
S	35	2,537.2	799.1	184,770.90	18,312.33	58,159.51	845.6475
M	57	5,379.7	1,598.4	511,367.03	45,029.14	151,696.73	3,627.1688
Phoenix Islands:							
S	35	2,383.6	757.8	163,903.38	16,512.26	51,994.83	1,573.4098
M	56	5,535.9	1,663.0	554,436.73	49,892.82	166,246.01	7,183.3584
L	46	6,207.1	1,738.5	841,039.55	65,959.63	235,434.15	3,472.3672
East Marshall Islands: *L*	38	5,180.2	1,434.9	708,885.88	54,390.23	196,334.36	2,715.5632
Bikini Island: *S*	31	1,829.9	587.3	109,843.77	11,263.09	35,156.10	1,826.5439
East Caroline Islands:							
S	60	3,916.3	1,216.9	259,183.29	24,959.13	80,411.50	3,559.8619
M	54	5,311.8	1,546.5	530,957.44	44,777.35	154,125.35	8,453.3800
L	55	7,685.0	2,136.2	1,080,633.32	83,369.90	300,077.18	6,829.2291
Central Caroline Islands:							
S	36	2,459.9	771.5	170,430.55	16.747.37	53,398.72	2,344.2164
M	101	10,204.4	2,979.7	1,042,507.06	88.623.57	303,814.74	11,519.1456
L	68	8,958.5	2,533.2	1,184,125.53	94,729.64	334,759.16	3,909.0264
Philippines (SW. Panay):							
S	241	15,702.8	5,088.9	1,035,302.60	108,524.29	335,066.42	12,157.6712
M	81	7,349.8	2,255.4	674,621.22	63,326.76	206,603.06	7,713.0714
L	32	4,257.3	1,233.6	568,957.89	47,760.94	164,733.11	2,564.0372
Japan: S	31	1,789.5	568.9	108,296.33	10,856.57	34,274.53	4,995.9994
Hawaii: [2]							
S	36	1,884.6	606.9	100,518.50	10,399.99	32,318.81	1,859.6900
M	34	3,466.4	1,025.2	356,040.12	31,093.84	105,169.90	2,630.4448
L	133	19,955.4	5,551.6	3,028,042.30	233.905.70	841,363.67	33,922.0808
Hawaii: [3]							
S	47	2,679.3	870.5	153,111.13	16,161.23	49,734.11	,373.9281
L	20	2,859.2	800.9	409,803.42	32,168.53	114,804.21	1052.1880
Northeast Africa: S	48	3,805.0	1,217.0	304,447.00	31,064.50	97,190.25	2,821.4792
Angola, Africa: [4]							
M	21	2,050.5	622.5	206,277.69	18,826.95	62,280.02	6,061.0115
L	27	3,717.0	1,065.6	215,125.62	42,276.26	147,542.99	3,418.6200
Y=greatest body depth:							
Costa Rica: [2] *M*	29	2,896.5	737.1	292,493.79	18,981.65	74,476.86	3,193.3676
109°–119° W.: *L*	21	3,146.2	813.0	475,009.34	31,865.56	122,976.02	3,648.6524
119°–129° W.: *L*	47	6,895.9	1,729.6	1,016,781.01	64,090.80	255,053.53	5,005.7588
129°–139° W.: *L*	46	6,667.6	1,673.6	988,059.18	62,388.60	248,086.74	21,605.0548
139°–149° W.: *L*	109	16,168.8	4,111.2	2,412,075.52	156,425.62	613,937.28	13,634.2958
East Line Islands:							
M	32	3,278.6	797.7	338,852.86	20,035.94	82,350.48	2,939.7988
L	154	22,339.4	5,580.4	3,255,028.66	203,481.16	813,560.86	14,452.0863
West Line Islands:							
S	43	2,947.9	736.8	204,526.51	12,786.92	51,111.30	2,430.8261
M	83	8,106.1	1,973.0	801,700.31	47,469.79	194,905.57	10,027.3316
L	57	7,876.2	1,949.6	1,094,133.62	67,274.94	271,142.41	5,808.5948
Phoenix Islands:							
S	36	2,428.3	602.8	165,447.87	10,182.66	41,030.24	1,652.2898
M	59	5,795.3	1,422.5	576,982.99	34,800.57	141,587.97	7,737.1918
L	44	5,943.0	1,478.5	806,235.34	49,956.87	200,558.37	3,525.1355
East Marshall Islands: *L*	39	5,314.9	1,318.7	727,070.77	44,873.79	180,554.56	2,758.9236
Bikini Island: *S*	31	1,829.9	453.4	109,843.77	6,729.06	27,179.80	1;826.5439
East Caroline Islands:							
S	60	3,916.3	974.8	259,183.29	15,994.84	64,346.21	3,559.8619
M	55	5,404.4	1,295.6	539,532.20	31,008.22	129,299.56	8,486.0298
L	56	7,837.2	1,949.7	1,103,798.16	68,456.67	274,743.15	6,982.0200

See footnotes at end of table.

TABLE A-3.—*Regression statistics of yellowfin tuna samples*—Continued

Character and size group [1]	N	SX	SY	SX^2	SY^2	SXY	Sx^2
Central Caroline Islands:							
S	37	2, 513. 9	620. 5	173, 346. 55	10, 554. 85	42, 751. 50	2, 544. 0309
M	102	10, 289. 2	2, 458. 5	1, 049, 698. 10	59, 904. 61	250, 653. 30	11, 780. 0938
L	71	9, 394. 9	2, 332. 8	1, 247, 581. 59	77, 105. 00	309, 934. 35	4, 424. 6040
Japan: *S*	30	1, 728. 2	450. 4	104, 538. 64	7, 083. 56	27, 201. 25	4, 982. 7987
Hawaii: [2]							
S	36	1, 884. 6	490. 7	100, 518. 50	6, 787. 50	26, 098. 06	1, 859. 6900
M	34	3, 466. 4	874. 9	356, 040. 12	22, 676. 15	89, 801. 52	2, 630. 4448
L	132	19, 792. 5	5, 011. 4	3, 001, 505. 89	193, 468. 40	761, 486. 24	33, 755. 4639
Northeast Africa: *S*	48	3, 805. 0	1, 006. 2	304, 447. 00	21, 317. 84	80, 536. 95	2, 821. 4792
Y=insertion ventral fin to anterior edge vent:							
109°–119° W.: *L*	17	2, 553. 6	739. 8	387, 099. 44	32, 482. 38	112, 090. 41	3, 518. 6777
119°–129° W.: *L*	47	6, 895. 9	1, 954. 4	1, 016, 781. 01	81, 621. 42	287, 958. 30	5, 005. 7588
129°–139° W.: *L*	46	6, 667. 6	1, 891. 8	988, 059. 18	79, 521. 56	280, 216. 10	21, 605. 0548
139°–149° W.: *L*	112	16, 636. 5	4, 704. 8	2, 484, 839. 89	198, 883. 76	702, 735. 61	13, 651. 2091
East Line Islands:							
M	33	3, 382. 8	934. 7	349, 710. 50	26, 706. 59	96, 615. 03	2, 942. 7473
L	153	22, 251. 1	6, 194. 2	3, 251, 069. 35	252, 070. 96	904, 976. 23	15, 046. 7931
West Line Islands:							
S	38	2, 600. 9	734. 4	179, 843. 35	14, 337. 12	50, 761. 20	1, 825. 4340
M	83	8, 070. 3	2, 240. 3	794, 878. 69	61, 207. 59	220, 517. 27	10, 183. 0022
L	56	7, 746. 7	2, 154. 5	1, 077, 363. 37	83, 350. 01	299, 562. 14	5, 731. 9256
Phoenix Islands:							
S	19	1, 309. 2	363. 7	90, 720. 80	7, 006. 19	25, 206. 01	510. 0295
M	49	4, 762. 2	1, 305. 9	469, 014. 30	35, 244. 71	128, 544. 55	6, 186. 7727
L	36	4, 834. 4	1, 353. 4	651, 354. 14	51, 091. 58	182, 369. 37	2, 147. 9356
East Marshall Islands: *L*	39	5, 321. 7	1, 479. 3	728, 908. 13	56, 402. 21	202, 694. 27	2, 741. 6970
East Caroline Islands:							
S	60	3, 916. 3	1, 120. 2	259, 183. 29	21, 192. 68	74, 090. 23	3, 559. 8619
M	54	5, 319. 5	1, 487. 0	532, 324. 19	41, 555. 98	148, 692. 69	8, 304. 1854
L	55	7, 699. 4	2, 146. 7	1, 084, 809. 32	84, 431. 95	302, 578. 93	6, 977. 3135
Central Caroline Islands:							
S	36	2, 438. 9	704. 0	167, 721. 55	13, 964. 26	48, 374. 98	2, 492. 8498
M	102	10, 289. 2	2, 884. 7	1, 049, 698. 10	82, 400. 69	293, 998. 80	11, 780. 0938
L	71	9, 404. 3	2, 598. 8	1, 249, 939. 11	95, 578. 08	345, 473. 82	4, 293. 2158

TABLE A-3.—*Regression statistics of yellowfin tuna samples*—Continued

Character and size group [1]	Sy^2	Sxy	$\bar{x}$	$\bar{y}$	b	a	s	$\hat{Y}$
X=fork legnth; *Y*=head length:								
Costa Rica: [2] *M*	173. 6283	731. 3128	99. 879	27. 238	0. 22901	4. 365	0. 477	27. 266
109°–119° W.: *L*	256. 5924	947. 8990	149. 819	37. 952	. 25979	. 969	. 738	35. 402
119°–129° W.: *L*	288. 3098	1, 137. 4179	146. 721	37. 002	. 22722	3. 664	. 815	35. 475
129°–139° W.: *L*	1, 120. 4244	4, 870. 2135	144. 948	36. 535	. 22542	3. 861	. 716	35. 420
139°–149° W.: *L*	837. 5227	3, 314. 7714	148. 713	37. 392	. 23760	2. 059	. 677	35. 323
East Line Islands:								
M	141. 6873	632. 2127	102. 509	27. 691	. 21484	5. 668	. 435	27. 152
L	836. 7488	3, 377. 1175	145. 319	36. 334	. 22802	3. 198	. 660	35. 121
West Line Islands:								
S	164. 8874	620. 6846	68. 707	19. 751	. 25221	2. 422	. 451	18. 816
M	553. 6904	2, 376. 9556	97. 758	26. 585	. 22125	4. 956	. 575	27. 081
L	342. 1867	1, 355. 1600	138. 179	35. 067	. 23330	2. 830	. 688	35. 492
Palmyra Island: [3]								
S	53. 8817	201. 4531	72. 491	20. 877	. 23822	3. 608	. 422	19. 092
M	173. 0948	772. 0569	94. 381	25. 379	. 21285	5. 290	. 399	26. 575
Phoenix Islands:								
S	102. 7173	404. 6286	67. 665	19. 330	. 23632	3. 339	. 450	18. 700
M	359. 7323	1, 618. 9492	98. 225	26. 434	. 20924	5. 881	. 607	26. 805
L	1, 103. 4174	4, 249. 3757	133. 533	33. 470	. 25534	—. 626	. 646	35. 122
East Marshall Islands: *L*	171. 7190	670. 2270	136. 335	33. 995	. 24251	. 932	. 492	34. 883
Bikini Island: *S*	106. 7697	437. 7271	59. 029	16. 803	. 23965	2. 657	. 254	18. 646
East Caroline Islands:								
S	200. 9099	838. 4362	65. 272	18. 268	. 23552	2. 895	. 244	18. 204
M	378. 4673	1, 779. 1837	98. 262	25. 664	. 20966	5. 062	. 320	26. 028
L	289. 6638	1, 281. 1993	139. 185	34. 674	. 21355	4. 951	. 556	34. 848
Central Caroline Islands:								
S	167. 7357	646. 6973	67. 943	18. 889	. 25420	1. 618	. 309	18. 141
M	564. 9781	2, 552. 7481	100. 875	26. 211	. 21670	4. 351	. 344	26. 021
L	290. 5322	1, 037. 7314	132. 258	33. 152	. 25250	—. 243	. 652	35. 107
Philippines (SW. Panay):								
S	850. 8985	3, 151. 3350	65. 192	18. 802	. 25770	2. 002	. 402	18. 753
M	371. 8277	1, 630. 8518	90. 738	24. 612	. 21144	5. 426	. 584	26. 570
L	138. 9072	485. 9244	132. 319	33. 909	. 23255	3. 138	. 929	35. 695
Japan: *S*	338. 5271	1, 295. 7323	57. 726	16. 410	. 25935	1. 439	. 292	18. 297
Hawaii: [2]								
S	134. 6856	496. 0800	52. 350	14. 839	. 26675	. 875	. 263	18. 214
M	134. 8224	570. 5241	101. 953	26. 859	. 21689	4. 746	. 588	26. 435
L	1, 772. 6468	7, 634. 8149	150. 041	37. 064	. 22507	3. 294	. 644	34. 804
Hawaii: [3]								
S	29. 2021	99. 5004	57. 006	16. 232	. 26610	1. 063	. 246	18. 360
L	84. 5580	291. 0780	142. 960	35. 710	. 27664	−3. 838	. 473	34. 892
Society Islands: *S*	69. 2153	264. 5365	58. 147	16. 729	. 25810	1. 721	. 250	18. 498
Northeast Africa: *S*	178. 0382	686. 5313	79. 146	22. 319	. 24332	3. 061	. 489	18. 877
Angola, Africa: [4]								
M	287. 9981	1, 310. 2386	97. 643	26. 690	. 21617	5. 583	. 501	27. 200
L	185. 5896	771. 5233	137. 667	35. 604	. 22568	4. 535	. 677	36. 130

See footnotes at end of table.

TABLE A-3.—*Regression statistics of yellowfin tuna samples*—Continued

Character and size group [1]	*Sy*²	*Sxy*	$\bar{x}$	$\bar{y}$	*b*	*a*	*s*	$\hat{Y}$
Y=pectoral fin length:								
Costa Rica: [2] *M*	134.4011	2.6800	2.9963	26.982	432.27201	−102.540	0.845	27.142
109°–119° W.: *L*	130.2295	1.7719	3.1378	36.095	556.09955	−140.400	1.292	34.554
119°–129° W.: *L*	244.9272	2.2620	3.1658	36.537	514.59869	−126.375	1.709	35.523
129°–139° W.: *L*	909.6983	15.8129	3.1547	35.878	512.96547	−125.947	1.497	35.437
139°–149° W.: *L*	331.2473	4.1885	3.1711	37.311	339.49066	−70.345	1.305	36.462
East Line Islands:								
M	416.4364	4.1211	3.1605	36.860	350.85434	−74.028	1.493	36.354
L	178.0487	2.9152	3.0083	28.681	532.81670	−131.606	.870	28.239
West Line Islands:								
S	221.2870	4.6018	2.8345	20.347	428.28557	−101.051	.768	19.421
M	813.2639	12.0643	2.9875	28.117	567.63026	−141.463	1.237	28.826
L	216.2000	2.9708	3.1398	36.250	529.81880	−130.103	1.044	36.583
Phoenix Islands:								
S	177.6027	3.3268	2.8282	20.322	461.18443	−110.110	.831	19.617
M	525.9023	7.8803	2.9878	29.243	546.83293	−134.140	1.3023	29.910
L	143.0861	1.7135	3.1292	35.717	496.03404	−119.502	1.149	36.555
East Marshall Islands: *L*	110.7138	1,0990	3.1337	36.038	366.96941	−78.959	1.361	36.493
Bikini Island: *S*	153.2794	3.4868	2.7677	18.026	410.25520	−95.520	.594	19.881
East Caroline Islands:								
S	365.2299	7.2406	2.8116	20.652	448.57046	−105.468	.835	20.710
M	520.3053	8.3698	2.9884	29.591	544.99401	−133,275	1.122	30.223
L	177.7255	2.5316	3.1456	36.791	398.77764	−88.648	1.204	36.811
Central Caroline Islands:								
S	301.7364	5.7481	2.8293	21.619	499.91303	−119.746	.650	20.875
M	705.1471	11.3351	3.0011	30.641	495.77274	−118.145	1.197	30.587
L	183.6188	1.7322	3.1207	35.779	376.72901	−81.787	1.300	36.736
Japan: S	534.0737	12.1384	2.7480	17.177	430.92565	−101.241	.627	19.974
Hawaii: [2]								
S	215.5789	4.5411	2.7154	15.295	433.19946	−102.336	.745	19.519
M	197.1306	2.4781	3.0068	29.129	517.42426	−126.450	1.467	28.777
L	927.9426	13.6475	3.1737	37.841	476.97184	−113.536	1.454	36.524
Society Islands: *S*	179.3229	3.0368	2.7570	17.829	556.67987	−135.648	.735	20.940
Northeast Africa: *S*	171.7448	3.4800	2.8962	20.698	407.32721	−97.272	.808	17.305
Angola, Africa: [4]								
M	463.4867	7.2230	2.9831	27.133	611.03638	−155.145	1.079	28.166
L	143.7067	1.7647	3.1374	35.322	588.40986	−149.286	1.263	35.834
Y=height second dorsal fin:								
Costa Rica: [2] *M*	.256956	.114971	2.9963	2.1899	1.93216	−3.5994	.0366	2.1971
109°–119° W.: *L*	.243691	.083607	3.1728	2.5851	2.66332	−5.8651	.0342	2.5140
119°–129° W.: *L*	.650678	.143601	3.1646	2.5985	3.29428	−7.8266	.0670	2.5375
129°–139° W.: *L*	1.623733	.661222	3.1540	2.5734	2.15071	−4.2099	.0685	2.5564
139°–149° W.: *L*	1.205756	.297734	3.1712	2.6373	2.46014	−5.1643	.0651	2.5755
East Line Islands:								
M	.253147	.087181	3.0069	2.2747	1.71269	−2.8752	.0588	2.2629
L	1.981966	.420403	3.1610	2.6642	3.00440	−6.8327	.0686	2.6194
West Line Islands:								
S	.310571	.166120	2.8366	1.9763	1.64155	−2.6801	.0308	1.9374
M	1.037693	.414389	2.9856	2.2504	2.04152	−3.8448	.0484	2.2798
L	.738760	.171563	3.1392	2.6188	2.99234	−6.7748	.0640	2.6394
Phoenix Islands:								
S	.270524	.130046	2.8284	1.9891	1.80376	−3.1127	.0325	1.9611
M	.497765	.222371	2.9866	2.2771	1.73367	−2.9007	.0460	2.3003
L	.425878	.106706	3.1275	2.6043	2.67467	−5.7607	.0578	2.6541
East Marshall Islands: *L*	.327443	.080457	3.1344	2.6502	2.71759	−5.8678	.0550	2.6820
Bikini Island: *S*	.219409	.126190	2.7646	1.8574	1.61455	−2.6062	.0237	1.9354
East Caroline Islands:								
S	.466530	.263826	2.8116	1.9812	1.63446	−2.6142	.0247	1.9834
M	.773031	.342603	2.9889	2.3076	2.10777	−3.9923	.0310	2.3310
L	.442076	.139895	3.1442	2.6805	2.11757	−3.9776	.0530	2.6845
Central Caroline Islands:								
S	.312898	.184815	2.8272	2.0107	1.63348	−2.6075	.0180	1.9873
M	1.102133	.472837	3.0011	2.3298	2.06809	−3.8767	.0353	2.3276
L	.626480	.125078	3.1205	2,6157	2.72033	−5.8731	.0644	2.6853
Japan: S	.660717	.430861	2.7506	1.8623	1.49317	−2.2448	.0245	1.9553
Hawaii: [2]								
S	.24851	.15071	2.7153	1.7985	1.44414	−2.1228	.0315	1.9394
M	.18846	.07539	3.0068	2.2678	1.66645	−2.7427	.0443	2.2566
L	2.13799	.69805	3.1737	2.6499	2.42564	−5.0484	.0583	2.5829
Society Islands: *S*	.202806	.102140	2.7531	1.8640	1.82837	−3.1697	.0299	1.9733
Northeast Africa: *S*	.180996	.084192	2.9054	2.0141	1.68539	−2.8826	.0309	1.8582
Angola, Africa: [4]								
M	.351508	.194019	2.9870	2.2290	1.73044	−2.9398	.0296	2.2515
L	.168917	.055379	3.1397	2.5297	2.09388	−4.0445	.0470	2.5431
Y=height anal fin:								
Costa Rica: [2] *M*	.286182	.120993	2.9964	2.2232	2.00041	−3.7708	.0412	2.2304
109°–119° W.: *L*	.328749	.087570	3.1723	2.6176	2.83931	−6.3895	.0667	2.5433
119°–129° W.: *L*	.557211	.126487	3.1656	-2.6382	2.85608	−6.4030	.0667	2.5825
129°–139° W.: *L*	1.689768	.676053	3.1530	2.6213	2.21454	−4.3611	.0677	2.6061
139°–149° W.: *L*	1.106309	.264215	3.1705	2.6827	2.200343	−4.2935	.0697	2.6290
East Line Islands:								
M	.313393	.110760	3.0088	2.3050	2.01323	−3.7524	.0540	2.2873
L	1.916956	.385379	3.1603	2.7098	2.85648	−6.3175	.0735	2.6693
West Line Islands:								
S	.343110	.177820	2.8361	1.9814	1.71601	−2.8854	.0308	1.9416
M	1.566031	.506854	2.9873	2.2942	2.37965	−4.8145	.0651	2.3245
L	.703209	.162075	3.1388	2.6726	3.17042	−7.2787	.0603	2.6958
Phoenix Islands:								
S	.338352	.145208	2.8281	1.9862	2.02152	−3.7309	.0358	1.9554
M	.702531	.272264	2.9884	2.3265	1.83379	−3.1536	.0602	2.3478
L	.309330	.071908	3.1266	2.6598	2.73654	−5.8963	.0524	2.7131
East Marshall Islands: *L*	.263563	.064190	3.1353	2.7137	2.45318	4.9778	.0535	2.7401
Bikini Island: *S*	.452704	.224620	2.7712	1.8631	1.90362	−3.4122	.0294	1.9425

See footnotes at end of table.

TABLE A-3.—*Regression statistics of yellowfin tuna samples*—Continued

Character and size group [1]	Sy^2	Sxy	$\bar{x}$	$\bar{y}$	b	a	s	$\hat{Y}$
East Caroline Islands:								
S	0.647966	0.313363	2.8116	1.9863	1.94135	−3.4720	0.0261	1.9888
M	.819340	.350096	2.9889	2.3532	2.15387	−4.0845	.0351	2.3771
L	.419122	.141299	3.1427	2.7392	2.22911	−4.2662	.0456	2.7468
Central Caroline Islands:								
S	.477109	.226364	2.8298	2.0155	1.97398	−3.5705	.0303	1.9821
M	1.198853	.484446	3.0020	2.3715	2.19595	−4.2207	.0369	2.3672
L	.478073	.109642	3.1202	2.6829	2.44464	−4.9449	.0556	2.7462
Japan: *S*	.804493	.464202	2.7544	1.8535	1.68668	−2.7923	.0277	1.9522
Hawaii: [2]								
S	.35863	.17991	2.7165	1.7726	1.81452	−3.1565	.0317	1.9476
M	.25928	.08162	3.0070	2.3009	1.82473	−3.1861	.0587	2.2881
L	2.16105	.70561	3.1737	2.6959	2.45174	−5.0852	.0574	2.6282
Society Islands: *S*	.204286	.098154	2.7558	1.8589	1.84795	−3.2337	.0367	1.9644
Northeast Africa: *S*	.255261	.094904	2.9054	2.0478	1.89983	−3.4720	.0427	1.8720
Angola, Africa: [4]								
M	.465751	.229392	2.9831	2.2316	1.94056	−3.5573	.0329	2.2644
L	.197757	.058162	3.1374	2.5594	1.82400	−3.1632	.0605	2.5753
Y=snout to insertion first dorsal fin:								
Costa Rica: [2] *M*	247.3317	875.6769	99.879	29.445	.27422	2.056	.517	29.478
109°–119° W.: *L*	273.6429	943.5086	149.819	41.229	.25859	2.487	1.249	38.690
119°–129° W.: *L*	297.6080	1,131.6557	146.598	40.557	.23818	5.641	.817	38.986
129°–139° W.: *L*	1,335.2524	5,309.5731	144.948	40.180	.24576	4.558	.831	38.964
139°–149° W.: *L*	1,065.7168	3,687.1724	148.617	40.830	.26423	1.561	.912	38.553
East Line Islands:								
M	190, 5364	726, 4491	102.509	29.736	.24686	4.431	.601	29.117
L	1,015.4022	3,624.0635	145.412	39.693	.24060	4.707	.968	38.391
West Line Islands:								
S	193.8216	666.9093	68.684	21.270	.27089	2.664	.560	20.272
M	662.5582	2,592.9605	97.701	28.595	2.41917	4.959	.648	29.151
L	368.3411	1,357.9180	137.760	37.613	.25409	2.610	.663	38.183
Palmyra Island: [3]								
S	68.7829	219.2757	72.491	22.786	.25930	3.989	.601	20.844
M	219.5772	861.7644	94.381	27.840	.23758	5.417	.519	29.175
Phoenix Islands:								
S	128.3457	438.3757	68.137	21.157	.28120	1.997	.392	20.275
M	453.8824	1,834.8211	98.225	28.659	.23714	5.366	.574	29.080
L	195.9245	767.8912	134.878	37.111	.22161	7,221	.774	38.246
East Marshall Islands: *L*	196.1190	711.5547	136.177	37.472	.26114	1.911	.528	38.471
Bikini Island: *S*	117.0019	455.4545	59.029	19.331	.24935	4.612	.344	20.820
East Caroline Islands:								
S	225.9424	863.8139	65.445	20.159	.25035	3.775	.412	20.048
M	489.4139	2,013.2142	98.262	28.378	.23724	5.066	.472	28.790
L	464.1772	1,722.2100	139.950	38.393	.24666	3.873	.854	38.405
Central Caroline Islands:								
S	173.4274	626.0369	67.963	20.851	.26946	2.538	.336	20.053
M	706.3275	2,811.4461	100.875	28.972	.23866	4.897	.595	28.763
L	278.6586	999.4995	132.455	36.587	.23281	5.750	.816	38.343
Philippines (SW. Panay):								
S	1,019.2827	3,379.1865	65.192	21.163	.27633	3.148	.597	21.109
M	428.3114	1,748.5687	90.738	27.562	.22670	6.992	.636	29.662
L	195.0534	625.5600	132.991	37.667	.24373	5.253	1.172	39.375
Japan: *S*	420.2387	1,442.2852	57.726	18.194	.28869	1.529	.365	20.294
Hawaii: [2]								
S	174.8700	562.9000	52.350	16.717	.30268	.872	.363	20.546
M	171.9026	631.9042	101.953	29.859	.24023	5.367	.792	29.390
L	2,072.9122	8,073.1400	149.698	41.066	.24585	4.263	.827	38.682
Hawaii: [3]								
S	36.0749	109.3328	57.006	17.757	.29239	1.089	.302	20.094
L	102.3400	308.8700	142.960	39.700	.29355	−2.266	.805	38.831
Society Islands: *S*	95.2982	323.5300	57.300	18.191	.28254	2.001	.441	20.366
Northeast Africa: *S*	236.4532	774.5938	79.146	24.656	.27453	2.928	.719	20.772
Angola, Africa: [4]								
M	326.8495	1,389.4743	97.643	28.895	.22925	6.510	.661	29.435
L	246.7608	882.9367	137.667	38.619	.25827	3.064	.865	39.222
Y=snout to insertion second dorsal fin:								
Costa Rica: [2] *M*	716.6532	1,497.4956	99.879	52.676	.46894	5.839	.731	52.733
109°–119° W.: *L*	845.0696	1,731.8520	149.819	76.195	.47466	5.082	1.101	71.534
119°–129° W.: *L*	1,004.2098	2,109.2262	147.061	73.998	.46092	6.215	.873	70.744
129°–139° W.: *L*	4,730.7931	10,065.2044	144.948	73.143	.46587	5.616	.973	70.838
139°–149° W.: *L*	3,362.0565	6,772.2915	148.807	74.748	.48159	3.084	.956	70.507
East Line Islands:								
M	676.3607	1,394.4728	102.509	52.724	.47387	4.148	.709	51.535
L	3,309.7462	6,849.5643	145.275	72.572	.45233	6.860	1.176	70.186
West Line Islands:								
S	575.4945	1,172.4419	68.556	36.933	.48232	3.867	.494	35.218
M	2,287.5234	4,870.4040	97.614	50.438	.46006	5.530	.747	51.536
L	1,308.7299	2,704.8159	138.084	69.073	.46798	4.452	.892	69.969
Palmyra Island: [3]								
S	180.7674	376.7145	72.615	39.091	.45521	6.036	.539	35.625
M	775.4415	1,650.5199	94.381	49.054	.45504	6.107	.666	51.611
Phoenix Islands:								
S	390.3168	793.6346	67.665	36.419	.46352	5.054	.801	35.183
M	1,640.9668	3,463.7556	98.225	50.476	.44768	6.503	1.259	51.271
L	796.5933	1,623.2620	134.937	67.628	.46748	4.548	.926	69.995
East Marshall Islands: *L*	638.2959	1,303.4785	136.454	68.610	.47543	3.736	.709	70.296
Bikini Island: *S*	418.3968	872.0206	59.029	32.058	.47742	3.876	.268	34.908
East Caroline Islands:								
S	786.0523	1,650.8019	65.156	34.966	.46999	4.343	.423	34.892
M	1.693.7611	3,778.2813	98.262	50.267	.44524	6.517	.466	51.041
L	1,533.9336	3,239.2500	139.950	69.311	.46394	4.383	.759	69.335

See footnotes at end of table.

TABLE A-3.—*Regression statistics of yellowfin tuna samples*—Continued

Character and size group [1]	Sy^2	Sxy	$\bar{x}$	$\bar{y}$	b	a	s	$\hat{Y}$
Central Caroline Islands:								
S	607.6519	1,234.3865	67.943	36.346	0.48521	3.379	0.499	34.918
M	2,474.9137	5,338.0030	100.829	51.292	.45397	5.519	.722	50.916
L	941.0570	1,849.3255	132.310	65.778	.47487	2.948	.976	69.430
Philippines (SW. Panay):								
S	3,128.0239	5,980.6878	65.194	36.963	.48909	5.077	.921	36.868
M	1,618.9233	3,478.0029	90.738	49.335	.45092	8.419	.801	53.511
L	496.8372	932.5000	132.625	68.771	.49348	3.323	1.283	72.410
Japan: *S*	1,301.1187	2,545.3652	57.726	31.594	.50914	2.203	.422	35.297
Hawaii: [2]								
S	511.6323	969.2300	52.350	28.928	.52118	1.644	.437	35.521
M	551.5250	1,186.0400	101.953	52.950	.45089	6.980	.724	52.069
L	7,299.8055	15,399.0719	149.829	74.636	.46475	5.003	1.049	70.068
Hawaii: [3]								
S	100.9362	189.9066	57.006	31.145	.50787	2.193	.316	35.205
L	300.1720	549.2740	142.960	71.880	.52203	−2.749	.864	70.335
Society Islands: *S*	265.0000	537.7300	57.586	31.700	.48560	3.736	.452	35.300
Northeast Africa: *S*	679.5392	1,309.8653	79.549	42.879	.49576	3.442	.828	35.666
Angola, Africa: [4]								
M	1,220.0315	2,708.2886	97.643	51.857	.44684	8.226	.720	52.910
L	797.1497	1,632.7434	137.667	70.104	.47760	4.354	.833	71.218
Y=snout to insertion anal fin:								
Costa Rica: [2] *M*	901.9325	1,689.1911	99.879	58.952	.52897	6.119	.558	59.016
109°–119° W.: *L*	1,030.0096	1,923.3681	149.819	84.105	.52714	5.129	.921	78.929
119°–129° W.: *L*	1,289.0966	2.483.5686	146.721	81.391	.49614	8.597	1.124	78.057
129°–139° W.: *L*	5,738.7524	11,092.3631	144.948	80.680	.51342	6.261	.997	78.140
139°–149° W.: *L*	4,079.4653	7,467.2943	148.773	82.568	.52850	3.941	1.095	77.931
East Line Islands:								
M	817.0247	1,518.4694	102.656	58.428	.52005	5.042	.955	57.047
L	4,131.1894	7,667.8075	145.368	80.998	.51604	5.987	1.074	78.233
West Line Islands:								
S	713.5600	1,305.8900	68.758	40.700	.53267	4.075	.662	38.699
M	2,875.5732	5,496.1261	97.735	55.655	.51179	5.635	.864	56.814
L	1,492.9556	2,855.7543	137.929	76.541	.50918	6.311	.848	77.596
Palmyra Island: [3]								
S	233.9869	435.8838	72.491	42.946	.51544	5.581	.531	39.085
M	903.3425	1,769.4060	94.381	53.851	.48782	7.810	.855	56.592
Phoenix Islands:								
S	444.3098	831.9653	67.953	39.997	.51940	4.702	.599	38.463
M	1,929.7416	3,813.6566	98.238	55.688	.49293	7.264	.944	56.557
L	989.7312	1,803.2645	135.082	74.456	.52593	3.412	.981	77.042
East Marshall Islands: *L*	856.0678	1,517.2455	136.335	75.068	.54898	.223	.780	77.080
Bikini Island: *S*	506.6084	957.7826	59.029	35.290	.52437	4.337	.388	38.421
East Caroline Islands:								
S	1,051.0974	1,923.1547	65.272	38.373	.54023	3.111	.458	38.226
M	2,045.6484	4,142.9923	98.385	55.228	.49083	6.938	.483	56.021
L	1,814.6219	3,462.6946	139.675	76.282	.51312	4.612	.845	76.449
Central Caroline Islands:								
S	764.8509	1,379.1509	67.943	40.243	.54211	3.410	.701	38.647
M	2,802.0358	5,668.0991	100.875	56.830	.48116	8.293	.865	56.409
L	1,179.7895	2,055.2489	132.019	72.647	.53493	2.026	1.104	76.916
Philippines (SW. Panay):								
S	3,750.4799	6,625.5577	65.192	40.489	.54181	5.167	.818	40,385
M	2,022.9023	3,895.0441	90.738	54.215	.50499	8.393	.842	58.892
L	500.3775	920.1875	132.552	75.852	.45201	15.937	1.706	79.218
Japan: *S*	1,552.8136	2,781.4510	57.726	34.561	.55674	2.423	.384	38.611
Hawaii: [2]								
S	598.5956	1,047.6500	52.350	31.789	.56335	2.298	.497	38.916
M	704.4953	1,337,5412	101.953	58.488	.50848	6.647	.873	57.495
L	8,665.5824	17,000.7218	150.068	82.924	.50137	7.684	1.045	77.876
Hawaii: [3]								
S	124.4687	210.5892	57.006	34.337	.56318	2.232	.361	38.839
L	337.0055	584.2480	142.960	79.985	.55527	.604	.836	78.342
Northeast Africa: *S*	792.1596	1,459.8564	79.098	47.460	.51834	6.460	.888	40.152
Angola, Africa: [4]								
M	1,512.1458	3,014.1629	7.643	56.986	.49730	8.428	.834	58.158
L	787.8897	1,508.4197	136.893	76.696	.50250	7.907	1.116	78.257
Y=snout to insertion ventral fin:								
109°–119° W.: *L*	293.8657	1,002.0157	149.819	42.186	.27463	1.041	.992	39.489
119°–129° W.: *L*	417.6371	1,330.6669	146.721	41.053	.26583	2.051	1.192	39.267
129°–139° W.: *L*	1,356.8898	5,353.5948	144.948	40.598	.24779	4.681	.830	39.372
139°–149° W.: *L*	1,032.2273	3,653.3615	148.773	41.489	.25857	3.021	.888	39.221
East Line Islands:								
M	171.8619	688.7797	102.681	30.816	.23594	6.589	.568	30.183
L	1,378.2468	4,281.4189	145.244	40.605	.28416	−.668	1.035	39.114
West Line Islands:								
S	197.7514	662.5486	68.798	21.986	.27978	2.738	.556	20.924
M	725.1524	2,662.0067	97.817	29.710	.25258	5.003	.802	30.261
L	419.3256	1,499.3643	138.129	39.591	.25849	3.886	.767	40.075
Palmyra Island: [3]								
S	67.7354	231.6094	72.491	22.831	.27388	2.977	.361	20.779
M	206.6390	838.6164	94.381	28.042	.23120	6.221	.481	29.341
Phoenix Islands:								
S	104.8074	386.4849	68.103	21.651	.24564	4.922	.547	20.889
M	507.6593	1,849.5511	98.855	29.696	.25748	4.243	.763	29.991
L	255.6681	846.2511	134.937	37.793	.24371	4.908	1.060	39.027
East Marshall Islands: *L*	207.6508	727.2816	136.321	37.760	.26782	1.250	.598	38.745
Bikini Island: *S*	136.5968	488.3494	59.029	18.945	.26736	3.163	.456	20.541
East Caroline Islands:								
S	278.3699	982.4089	65.272	20.282	.27597	2.269	.354	20.207
M	487.3084	2,001.3000	98.367	28.639	.23674	5.352	.510	29.026
L	399.8920	1,591.7800	139.727	38.840	.23308	6.272	.738	38.903

See footnotes at end of table.

TABLE A-3.—*Regression statistics of yellowfin tuna samples*—Continued

Character and size group [1]	Sy^2	Sxy	$\bar{x}$	$\bar{y}$	b	a	s	$\hat{Y}$
Central Caroline Islands:								
S	213.6964	681.6964	68.331	21.431	0.29080	1.560	0.674	20.462
M	716.5196	2,764.7333	101.034	29.502	.24001	5.253	.731	29.254
L	360.4895	1,028.6865	131.743	37.253	.26316	2.584	1.166	39.426
Philippines (SW. Panay):								
S	1,068.2601	3,489.7440	65.157	21.116	.28704	2.413	.528	21.071
M	526.4000	1,951.9623	90.738	27.844	.25307	4.881	.641	30.188
L	205.6600	614.1950	133.041	38.550	.23954	6.681	1.397	40.217
Japan: *S*	416.3374	1,434.3187	57.726	18.352	.28709	1.779	.396	20.440
Hawaii: [2]								
S	168.6675	547.5950	52.350	16.858	.29445	1.444	.467	20.583
M	181.0448	647.7448	101.953	30.153	.24625	5.047	.820	29.672
L	2,174.4026	8,398.2667	150.041	41.741	.24758	4.594	.852	39.255
Hawaii: [3]								
S	38.4587	110.0536	57.006	18.521	.29432	1.743	.367	20.874
L	96.4895	307.5460	142.960	40.045	.29229	−1.741	.605	39.180
Northeast Africa: *S*	208.4792	717.6459	79.146	25.229	.25435	5.098	.751	21.631
Angola, Africa: [4]								
M	374.2714	1,497.3414	97.643	29.643	.24704	5.521	.479	30.225
L	220.5800	845.3900	137.667	39.467	.24729	5.423	.679	40.044
Y=greatest body depth:								
Costa Rica: [2] *M*	246.6014	855.8203	99.879	25.417	.26800	−1.351	.799	25.449
109°–119° W.: *L*	390.8457	1,173.1343	149.819	38.714	.32153	−9.457	.848	35.557
119°–129° W.: *L*	441.5200	1,284.4100	146.721	36.800	.25659	−.847	1.577	35.076
129°–139° W.: *L*	1,498.6661	5,502.0583	144.948	36.383	.25467	−.530	1.488	35.124
139°–149° W.: *L*	1,361.7169	4,091.6786	148.338	37.717	.30010	−6.799	1.118	35.215
East Line Islands:								
M	150.7747	621.1294	102.456	24.928	.21128	3.281	.807	24.409
L	1,267.7564	4,062.2382	145.061	36.236	.28108	−4.538	.910	34.813
West Line Islands:								
S	161.9377	599.3763	68.556	17.135	.24657	.231	.587	16.258
M	569.4407	2,214.7833	97.664	23.771	.22087	2.200	.995	24.287
L	591.7793	1,748.7343	138.179	34.204	.30106	−7.396	1.090	34.752
Phoenix Islands:								
S	89.1089	369.7056	67.453	16.744	.22375	1.651	.433	16.195
M	503.8539	1,862.3048	98.225	24.110	.24070	.467	.988	24.537
L	275.9098	860.0632	135.068	33.602	.24398	.648	1.254	34.805
East Marshall Islands: *L*	284.8236	842.8003	136.279	33.813	.30548	−7.818	.860	34.949
Bikini Island: *S*	97.7194	416.0368	59.029	14.626	.22777	1.181	.319	15.986
East Caroline Islands:								
S	157.5893	719.3893	65.272	16.247	.20208	3.057	.459	16.192
M	488.5953	1,991.5484	98.262	23.556	.23469	.495	.632	23.964
L	575.7756	1,882.6350	139.950	34.816	.26964	−2.920	1.123	34.830
Central Caroline Islands:								
S	148.8973	592.7176	67.943	16.770	.23298	.941	.556	16.085
M	647.5291	2,653.3177	100.875	24.103	.22524	1.382	.706	23.906
L	457.7347	1,252.3399	132.323	32.856	.28304	−4.597	1.223	35.020
Japan: *S*	321.5547	1,255.2073	57.607	15.013	.25191	.501	.437	16.875
Hawaii: [2]								
S	98.9864	409.9150	52.350	13.631	.22042	2.092	.504	16.419
M	162.8941	602.8918	101.953	25.732	.22920	2.364	.879	25.284
L	3,209.8397	10,060.9787	149.943	37.965	.29805	−6.726	1.274	35.001
Northeast Africa: *S*	225.3725	774.6375	79.146	20.837	.27455	−.893	.525	16.953
Y=insertion ventral fin to anterior edge vent:								
109°–119° W.: *L*	288.0247	963.7465	150.212	43.518	.27389	2.376	1.267	40.721
119°–129° W.: *L*	351.6464	1,206.2371	146.721	41.583	.24097	6.228	1.164	39.964
129°–139° W.: *L*	1,719.2287	6,003.8027	144.948	41.126	.27776	.865	1.075	39.751
139°–149° W.: *L*	1,248.5543	3,883.7779	148.540	42.007	.28450	−.253	1.143	39.577
East Line Islands:								
M	231.9206	799.7827	102.509	28.324	.27178	.464	.685	27.642
L	1,298.9754	4,141.1737	145.432	40.485	.27522	.459	1.027	38.990
West Line Islands:								
S	143.8737	495.3853	68.445	19.326	.27138	.751	.512	18.391
M	738.3841	2,687.2328	97.233	26.992	.26389	1.333	.601	27.722
L	459.4699	1,521.6909	138.334	38.473	.26548	1.748	1.014	38.915
Phoenix Islands:								
S	44.2063	145.1658	68.905	19.142	.28462	−.470	.412	18.030
M	441.1425	1,627.0607	97.188	26.651	.26299	1.092	.531	27.391
L	211.2589	622.7878	134.289	37.594	.28995	−1.343	.950	39.250
East Marshall Islands: *L*	291.2231	838.0954	136.454	37.931	.30568	−3.780	.973	39.015
East Caroline Islands:								
S	278.5460	972.9090	65.272	18.670	.27330	.831	.467	18.596
M	608.4060	2,209.4215	98.509	27.537	.26606	1.328	.629	27.934
L	644.2975	2,064.3486	139.989	39.031	.29587	−2.388	.795	39.034
Central Caroline Islands:								
S	197.1489	680.9356	67.747	19.556	.27316	1.050	.573	18.805
M	817.7146	3,006.1016	100.875	28.281	.25518	2.540	.709	28.058
L	454.6795	1,249.9491	132.455	36.603	.29115	−1.961	1.147	38.800

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[1] *S*, small, less than 80 cm., compared at length of 65 cm.; *M*, medium, 80 to 120 cm., compared at length of 100 cm.; *L*, large, over 120 cm., compared at length of 140 cm.

[2] Schaefer (1952). [3] Godsil and Greenhood (1951). [4] Schaefer and Walford (1950).

ORIGINS OF HIGH SEAS SOCKEYE SALMON

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ABSTRACT

To fulfill the requirements of the Protocol of the International North Pacific Fisheries Treaty, Canada, Japan, and the United States undertook a program of offshore fishery research in the North Pacific Ocean and Bering Sea. The studies have contributed much to understanding the distribution and migrations of sockeye salmon, *Oncorhynchus nerka* (Walbaum), at sea. The main objective of this report is to examine the available information concerning the origin of sockeye salmon that are found in different parts of the ocean. Several techniques have been successfully used to identify the sources of fish at sea. These include studies of parasites, movements of tagged fish, and scale differences and other morphological characteristics. The last provides most of the basis for quantitative statements regarding origin. Nearly all of the field work was done between early May and late September; accordingly results are available for only this period. It was found that in early summer the maturing sockeye salmon north and south of the eastern and central Aleutian Islands were mainly of Bristol Bay, Alaska origin.

The Protocol to the International Convention for the High Seas Fisheries of the North Pacific Ocean states that "The Commission to be established under the Convention shall, as expeditiously as practicable, investigate the waters of the Convention area to determine if there are areas in which salmon originating in the rivers of Canada and of the United States of America intermingle with salmon originating in the rivers of Asia. If such areas are found, the Commission shall conduct suitable studies to determine a line or lines which best divide salmon of Asiatic origin and salmon of Canadian and United States of America origin . . ."

The International North Pacific Fisheries Commission (INPFC) has undertaken research for the purpose of satisfying the requirements of the protocol to the treaty. As provided by the treaty, extensive research has been conducted by Canada, Japan, and the United States in a cooperative manner. This has resulted in greatly improved understanding of the distribution of salmon at sea.

While much remains to be done in the analysis of the available data, it is worthwhile now to examine the results of the research pertinent to the protocol problem. This report deals with the sockeye salmon, *Oncorhynchus nerka* (Walbaum), one of the more important species of salmon found in the waters of the North Pacific Ocean.

The purposes here are to review the pertinent research and combine the results so that the distribution and origins of sockeye salmon in the high seas can be clarified. While this is principally concerned with the Commission's studies, reports from other sources are incorporated as well.

LIFE HISTORY

A brief review of the life history of sockeye salmon provides a background for understanding the studies to be discussed. The distribution of spawning grounds, the homing habit, the length of time spent in the sea, and other characteristics of the species control to a high degree the salmon's ocean distribution and migrations.

The sockeye salmon reproduces in streams entering the sea from the Kurile Islands (fig. 1) to the

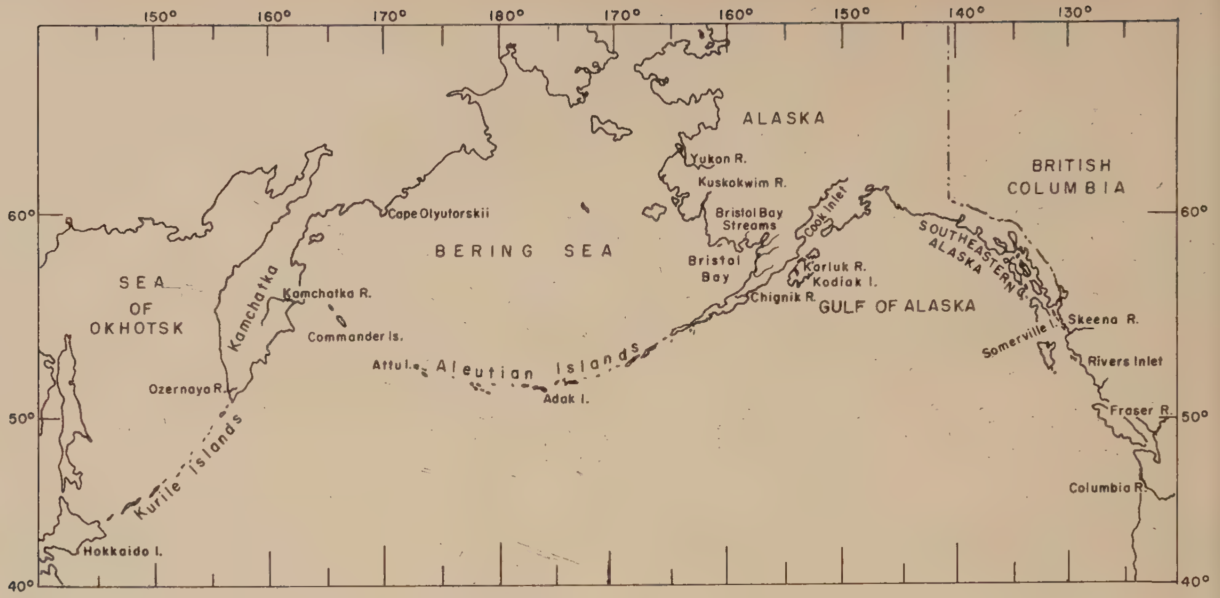
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°
40°
ALASKA
BRITISH COLUMBIA
Yukon R.
Kuskokwim R.
Bristol Bay Streams
Cook Inlet
Cape Olyutorskii
BERING SEA
Bristol Bay
Karluk R.
Kodiak I.
Chignik R.
GULF OF ALASKA
SOUTHEASTERN ALASKA
SEA OF OKHOTSK
Kamchatka
Kamchatka R.
Commander Is.
Attu I.
Aleutian Islands
Adak I.
Somerville I.
Skeena R.
Rivers Inlet
Fraser R.
Columbia R.
Ozernaya R.
Kurile Islands
Hokkaido I.

FIGURE 1.—Reference map.

northern Bering Sea[1] coast of Asia, and from the Columbia River to the northern Bering Sea coast of North America. The larger and more valuable populations tend to occur in the central portions of the species' range between lat. 49° and 60° N. According to Taguchi (1956) Asian sockeye originate preponderantly in southwest Kamchatka (mainly Ozernaya River) and in the Kamchatka River in east central Kamchatka. These two areas provided about 87 percent of the inshore Japanese catch of this species for the years 1932–41, inclusive. In North America the Bristol Bay tributaries in the north and the Fraser River in the south provide the largest stocks of sockeye. From 1955 to 1959 an average of 64 percent of the North American catch were salmon destined for these streams. The streams lying between the Fraser River and Bristol Bay produced almost all of the remaining 36 percent.

Sockeye salmon are usually found only in those river systems that have suitable lake areas for growth of the young prior to seaward migration. While this is not always the case, there appears to be no major sockeye population that does not spawn so that the young have easy access to a lake either below the spawning grounds or not far upstream.

The adult salmon spawn in the summer or autumn. The timing appears to be connected with the temperature regimen of the spawning grounds (Royal, 1953). Because a specific range of temperatures and quantity of heat are needed to complete development within the egg at an appropriate time, spawning must occur in water that is within a favorable range of temperatures and at a suitable point in the annual temperature cycle if the young organism is to survive in its environment.

Temperature requirements are a major reason for the very strong tendency of sockeye salmon to return to the tributary, and even to that part of the tributary, in which they were hatched. There is evidence that a fish from one spawning ground generally would not reproduce as successfully in another with a different temperature regime (Royal, 1953; Andrew and Geen, 1960). Because the time of spawning is set by conditions on the ancestral spawning ground, time of migration from the sea is also influenced. The fish must arrive while river conditions are suitable for migration and must have time to complete their fresh-water migration to the spawning grounds which may be hundreds of miles from the ocean.

The precise adaptation to particular spawning grounds and the strong "homing instinct" have given rise to numerous independent or semi-independent populations of sockeye salmon. Within the Fraser River in Canada, for example, there are at least 29 unique, distinguishable populations that reproduce and flourish or fail as independent units (International Pacific Salmon Fisheries Commission, 1961). The number of minor populations and subunits is certainly greater. Krogius (1958) inferred that the same situation exists in the Kamchatka River. Studies by Roos[2] showed that the sockeye runs of the Chignik River on the south side of the Alaska Peninsula are composed of two major stocks that enter the river at different times. The early part of the run proceeds to Black Lake tributaries and the later arriving fish spawn in the tributaries of Chignik Lake.

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[1] The Bering Sea is considered here as a separate body of water and not referred to as a part of the North Pacific Ocean.

Stream residence is brief. The eggs are deposited in stream or lake gravels that have an adequate flow of aerated water through them. The young emerge in spring. Ordinarily, the young do not remain in the stream, but promptly migrate to the lake. Except for a small number of races in which the young migrate to the sea shortly after emerging from the gravel, lake residence is characteristic of the species.

Length of lake residence varies considerably between lakes and races. Most often, the young will spend 1 or 2 years in the lacustrine environment and migrate to sea in the first or second spring following the year of hatching. In some lakes, however, the young may remain for 3 or even 4 years. The length of fresh-water residence is a characteristic of the race and its lake. Often a lake may have seaward migrants of several different ages. Usually, the older migrants from a lake are larger than the younger migrants.

During life in the lake, young sockeye compete with other fish for food and are preyed upon by larger fish and birds. The number of seaward migrants forms a small but variable portion of the number of eggs carried into a lake system by adult females. Foerster (1955) has given an average value of 1–2 percent for British Columbia sockeye salmon.

The migration from the lake to the sea is mainly in April, May, and June. The young salmon appear to move downstream rapidly without protracted delay enroute except where a chain of lakes must be passed. In many systems migration seems to occur only during darkness, and the migrants rest in quiet areas in daylight.

From one to several years are spent growing and maturing in the sea. Fish which return after a single winter at sea are almost always small males, about 3 pounds in weight in the Fraser River (Killick and Clemens, 1963). Some races seem to have large numbers of these precocious individuals, while in other races they are rarely seen. Most commonly, the sockeye returns after 2 or 3 winters in the ocean and occasionally after 4 winters. The average size of the fish at the time of migration to the natal stream seems to depend to some extent upon the race, location of the spawning grounds, timing of the run, and length of sea life.

The time at which the adults re-enter their home stream is an inherited characteristic of the particular race and varies from May to September among the diverse groups. When eggs from one river have been reared in a hatchery (on some occasions far from the native stream) and released in a stream or lake other than that in which they originated, transplanted fish retain a migration timing comparable to that of their parents (Andrew and Geen, 1960). Choice of unsuitable donor stocks has been known to result in disastrously bad timing of the return.

Upon entering the stream, the adults move swiftly upstream until they reach the vicinity of the spawning grounds. Here they may spawn almost immediately or linger in the lakes or the quiet waters of the larger streams for more than a month before spawning. After spawning the salmon die.

INSHORE DISTRIBUTION

It is necessary to examine the inshore distribution, abundance, and timing because of their effect upon the distribution and abundance of sockeye salmon at sea. The area through which they are distributed must at some time include the sea approaches to their home stream. The timing of the migrations is such that the maturing fish disappear from the sea at differing times according to their race. Because the maturing fish on the high seas are the same fish that appear in the rivers a short time later, there is a strong relationship between the abundance in the rivers and the abundance at sea, although this relationship may be modified by fishing at sea.

ABUNDANCE

For the Columbia, Fraser, Skeena, Karluk, Chignik, Ozernaya, and the Bristol Bay Rivers, the number of fish returning to the stream is known for some years, but for most other streams the number of fish in the runs is unknown or unavailable. Consequently, it is not possible to make comparisons of abundance on the basis of the total number of fish migrating to the stream. The best available common index of the abundance (catch plus escapement) of sockeye salmon in rivers of Asia and North America is the catch. For most recent years catch data have been published for the major fishing areas. In making comparisons of the runs to various areas we should keep in mind that these comparisons are based on the assumption that fishing removes the same portion of the salmon from the stock of each area. This assumption is known to be not strictly true. At various times fishery regulation has severely reduced the part of the run taken in all of the streams on the North American continent. While the extent of regulatory reduction in fishing is not as readily available for Asian streams, we can be certain that stream fishing has been curtailed there as well. According to Krogius and Krokhin (1956), the Kamchatka River fishing has been limited to a very low level since 1951. From 1940 to 1955 the catch in the Ozernaya River fishery has varied from 32 to 85 percent of the run (Semko, 1961).

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[2] Roos, John F., Red Salmon Studies—Chignik, Fisheries Research Institute, College of Fisheries, University of Washington, Seattle, Contribution No. 77, March 1960, pp. 7–8.

Table 1 gives the sockeye salmon catch by nation for the years 1909–60. It is immediately apparent that the data do not allow close comparison before 1933 or for 1937 to 1939 because records are incomplete. Following 1952 the high seas mothership salmon fishery expanded rapidly and we are again not able to make comparisons. By 1954 the greater part of the catch by Asian nations was taken by Japan on the high seas; in 1957 the greater part of the world catch was so taken (table 2). High seas catch data have not been available in the detail necessary to accurately assign fish to the mainland areas from which they originated. In addition, the part of the catch which would not have matured in the year of capture is unknown. For these reasons, it is not possible here to credit the high seas catch to inshore areas of origin or year of spawning, and there are no means available for making comparisons of the numbers of fish produced by the various rivers even if inshore catch and escapement were known. As will be shown later, the high seas catch is taken primarily from Asian and Bristol Bay stocks of sockeye salmon. For these stocks the high seas catch exceeded the inshore catch in 1955, 1957, 1958, and 1959.

TABLE 1.—*Catch of sockeye salmon in millions of fish* [1] [2]

[Millions of fish]

Year	Coastal catch		Mothership fishery Japan	Total catch by Japan-U.S.S.R.	Coastal catch		Total catch by Canada-U.S.A.	Total catch
	U.S.S.R.	Japan [3]			Canada	U.S.A.		
1909	--------	1.3	--------	(1.3)	--------	--------	--------	--------
1910	--------	1.9	--------	(1.9)	--------	--------	--------	--------
1911	--------	1.8	--------	(1.8)	--------	--------	--------	--------
1912	--------	1.3	--------	(1.3)	--------	--------	--------	--------
1913	--------	2.5	--------	(2.5)	--------	--------	--------	--------
1914	--------	0.9	--------	(0.9)	--------	--------	--------	--------
1915	--------	2.0	--------	(2.0)	--------	--------	--------	--------
1916	--------	2.9	--------	(2.9)	--------	--------	--------	--------
1917	--------	2.4	--------	(2.4)	--------	--------	--------	--------
1918	--------	4.6	--------	(4.6)	--------	--------	--------	--------
1919	--------	5.7	--------	(5.7)	--------	--------	--------	--------
1920	--------	4.2	--------	(4.2)	4.3	20.2	24.5	(28.7)
1921	--------	5.7	--------	(5.7)	2.2	26.2	28.4	(34.1)
1922	--------	10.6	--------	(10.6)	4.0	35.0	39.0	(49.6)
1923	--------	8.3	--------	(8.3)	4.5	28.1	32.6	(40.9)
1924	--------	8.2	--------	(8.2)	5.0	19.9	24.9	(33.1)
1925	--------	4.3	--------	(4.3)	5.0	17.0	22.0	(26.3)
1926	--------	6.6	--------	(6.6)	4.2	31.2	35.4	(42.0)
1927	--------	[4] 9.8	--------	(9.8)	4.1	18.8	22.9	(32.7)
1928	--------	[4] 15.4	--------	(15.4)	2.4	28.4	30.0	(46.2)
1929	--------	[4] 11.2	--------	(11.2)	3.6	20.9	24.5	(35.7)
1930	--------	[4] 12.4	0.3	(12.7)	5.3	14.9	20.2	(32.9)
1931	--------	[4] 9.7	(0.6)	(10.3)	3.1	24.2	27.3	(37.8)
1932	--------	[4] 9.0	(1.3)	(10.3)	3.6	28.0	31.6	(41.9)
1933	--------	[4] 5.9	2.9	8.8	3.6	33.2	36.8	45.6
1934	--------	[4] 12.5	7.5	20.0	4.6	36.1	40.7	60.7
1935	--------	[4] 4.8	3.4	8.2	4.6	11.2	15.8	24.0
1936	--------	[4] 7.9	7.0	14.9	4.9	36.2	41.1	56.0
1937	--------	5.7	10.3	(16.0)	4.6	32.1	36.7	(52.7)
1938	--------	7.0	9.7	(16.7)	5.1	37.0	42.1	(58.8)
1939	--------	5.0	9.2	(14.2)	4.1	25.3	29.4	(43.6)
1940	[5] 1.3	3.7	5.3	10.3	4.2	13.0	17.2	27.8
1941	[5] 1.7	3.9	5.1	10.7	5.3	17.6	22.9	33.6
1942	[5] 2.1	3.6	7.3	13.0	7.9	16.1	24.0	37.0
1943	[5] 3.0	2.4	2.9	8.3	2.1	26.7	28.8	37.1
1944	3.5	1.4	0.3	5.2	2.0	20.6	22.6	29.1
1945	4.4	--------	--------	4.4	3.8	15.9	19.7	24.1
1946	4.9	--------	--------	4.9	7.1	18.1	25.2	30.1
1947	3.8	--------	--------	3.8	3.9	26.3	30.2	34.0
1948	2.3	--------	--------	2.3	2.8	20.8	23.6	25.9
1949	3.3	--------	--------	3.3	3.0	13.1	16.1	19.4
1950	3.4	--------	--------	3.4	4.5	15.2	19.7	23.1
1951	2.9	--------	--------	2.9	4.4	10.8	15.2	18.1
1952	3.4	--------	0.7	4.1	4.9	18.2	23.1	27.2
1953	1.9	--------	1.6	3.5	5.9	14.0	19.9	23.4
1954	1.5	--------	3.8	5.3	6.7	14.3	21.0	26.3
1955	1.1	--------	12.5	13.6	2.8	9.6	12.4	26.0
1956	2.1	--------	10.3	12.4	3.3	15.7	19.0	31.4
1957	1.3	--------	20.1	21.4	3.0	11.6	14.6	36.0
1958	0.4	--------	12.0	12.4	12.0	11.6	23.6	36.0
1959	1.5	--------	9.1	10.6	3.3	9.9	13.2	23.8
1960	[6] 1.5	--------	[7] 12.9	14.4	[7] 2.9	[7] 19.2	22.1	36.5

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[1] From Progress Report—catch statistics for North Pacific Salmon. International North Pacific Fisheries Commission, Vancouver, B.C. (INPFC Doc. 398), October 1960, 15 pp.

[2] Figures in parentheses are incomplete.

[3] Catch from fisheries on coast of U.S.S.R.

[4] Combined Japan-U.S.S.R. catch.

[5] From Pacific Salmon Catch Statistics of the Union of Soviet Socialist Republics, 1940-58, International North Pacific Fisheries Commission Secretariat, Vancouver, B.C., (INPFC Doc. 286, Revision 1), July 1961, 4 pp.

[6] From Statistical Information on coastal catch of Far Eastern salmon by the Soviet Union for the year 1960. International North Pacific Fisheries Commission, Vancouver, B.C. (INPFC Doc. 457), July 1963, 284 pp. [Processed]; average weight of 2.6 kg. per fish used to convert weight to number of fish.

[7] From Kasahara and Kissack (1961). See footnote 4, p. 451.

Let us examine the years for which complete catch figures are available. In table 1, the years 1933–36 and 1940–52 inclusive can perhaps best be used for this comparison. In the years 1933–52 the mothership catches were made near Kamchatka

TABLE 2.—*High seas and total world catch of sockeye salmon* [1]

[Millions of fish]

Year	Total	High seas only	High seas catch as percent of whole
1952	27.2	0.7	2.6
1953	23.4	1.6	6.8
1954	26.3	3.8	14.4
1955	26.0	12.5	48.1
1956	31.4	10.3	32.8
1957	36.0	20.1	55.8
1958	36.0	12.0	33.3
1959	23.8	9.1	38.2
1960	36.5	12.9	35.3

[1] Derived from table 1.

TABLE 3.—*Inshore catch of sockeye salmon by area of origin*

[Thousands of fish]

Year	East Kamchatka [1]	West Kamchatka [2]	Bristol Bay [3]	Chignik River [4]	Karluk River [5]	Skeena River [6]	Fraser River [7]
1944	1,808	1,808	11,546	945	641	762	1,439
1945	3,000	1,615	7,300	553	676	1,165	1,675
1946	2,423	2,654	8,051	791	228	591	7,791
1947	2,308	1,615	18,663	1,971	110	363	443
1948	692	1,692	14,544	375	657	1,131	1,842
1949	192	3,192	6,449	543	450	737	2,078
1950	423	3,153	7,157	317	504	530	2,115
1951	269	2,692	4,327	257	149	689	2,425
1952	115	3,423	11,266	140	219	1,282	2,267
1953	38	1,923	6,112	301	77	246	4,024
1954	154	1,385	4,653	91	95	571	9,529
1955	269	923	4,549	350	4	157	2,115
1956	500	1,692	8,881	676	75	149	1,802
1957	231	1,115	6,276	306	91	280	3,050
1958	154	231	2,986	321	148	602	15,200
1959	577	962	4,608	428	118	196	3,393

[1] Progress Report-catch statistics for North Pacific Salmon. International North Pacific Fisheries Commission, Secretariat, Vancouver, B.C. (INPFC Doc. 389), October 11, 1960, 15 pp.; mainly Kamchatka River.

[2] From INPFC Doc. 389; mainly Ozernaya River.

[3] From Bristol Bay Sockeye Salmon catch in numbers of fish by river system—1893–1960, International North Pacific Fisheries Commission, Secretariat (INPFC Doc. 444), Dec. 7, 1960, 2 pp.; includes Ugashik, Egegik, Naknek, Kvichak, Nushagak, and Togiak Rivers.

[4] From U.S. Fish and Wildlife Service (1946–53); Simpson (1960).

[5] 1944–53 from Rounsefell (1958); 1954–59 from Simpson (1960).

[6] 1944–52 from Foskett (1953) converted at 67 pounds of raw fish per case; 1953–59 from Department of Fisheries, Canada.

[7] From INPFC Doc. 389; INPFC Annual Report, 1959.

and probably were almost all, if not entirely, Asian sockeye salmon. During these years the total catch varied from 18 to 61 million sockeye salmon. The percentage of Asian fish in the total catch varied from 9 to 37 percent with a 17-year mean of 23 percent. The Asian portion of the total recorded catch for the other years from 1920 to 1945 in each instance falls within the limits given above. In other words, for the years for which the continent of origin appears certain, the catch of Asian sockeye salmon was generally less than one-third of the total and averaged about one-fourth.

The inshore catch of salmon has generally declined in the years between 1920 and 1960. In the 20 years 1920–39 the total catch averaged 41 million fish (table 1); from 1940 to 1959 it averaged 28 million fish. This decline has not been uniform. Some streams on the American continent have had runs of more or less the same size throughout the period. In Asia, the sockeye catches have dropped to low levels in recent years (table 3). Information available for the Kamchatka River shows that in 1948 the catch suddenly declined to a fraction of its former size. In North America, the trend of catch in Bristol Bay and in the Chignik and Karluk Rivers has been generally downward. The runs to the Skeena River in Canada were relatively stable until a landslide in the Babine River in 1951 (removed in 1952–53) interfered with the passage of adult fish. A similar fate befell the Fraser River in 1913. The runs of Fraser River sockeye dwindled thereafter until means of upstream passage were provided in 1946. Since then, the numbers of fish have been restored to a large degree.

Although the inshore catch records are not complete, and the fishing intensities on the stocks of the various rivers may not be equal, the catch records are the best available data for comparing the relative abundance of the fish between North American and Asian streams. In the years for which comparable records are shown, the average portion of the world catch originating in Asian streams was 23 percent; and in North American streams, 77 percent. In the past several decades the stocks of most major streams have tended to decline. In the 6 years beginning with 1955, from 33 to 56 percent of the world catch was made on the high seas and cannot now be assigned to stream or spawning year.

TIMING

The time of arrival of sockeye salmon at their natal streams is quite consistent for each stream, but varies between streams. Asian streams are typical in this respect. Taguchi (1956) showed that the greater part of the Asian sockeye population is produced by the Ozernaya and Kamchatka Rivers. Let us then consider the arrival of adults making up these runs. The Ozernaya River sockeye arrival may be determined by the periods given for the Yavina fishery (Taguchi, 1956). The run lasts from June 30 to August 30 of each year, and the peak of the run occurs between July 25 and August 5. The percent of the run represented in the period containing the peak is not clear, but about 70 percent of the catch was made during the last 10 days of July and the first 10 days of August. The run to the other major sockeye producing area of Asia, the Kamchatka River, arrives at that stream somewhat earlier. Taguchi stated that the Kamchatka River run lasts from June 9 to September 5, and peaks between June 13 and July 5. The peak interval appears to account for about 75 percent of the fish, with only 22 percent of the catch shown as taken before June 1 or after July 1. Birman (1958) stated that the Kamchatka River run finishes mainly on July 25 and the principal migration in the Ozernaya begins in the first days of August. In fact, the run is nearly over in the Kamchatka River when the bulk of the run appears in the Ozernaya River.

The peaks of the runs in the minor fisheries of northwestern Kamchatka and the Okhotsk Sea coast generally occur between mid-July and mid-August according to Taguchi. In this respect they resemble the Ozernaya more than the Kamchatka River. The peak period for the minor fisheries for sockeye salmon in northeastern Kamchatka is between June 28 and July 12, and appears to resemble the Kamchatka River fisheries in timing. The Asian sockeye salmon may, therefore, be placed into two broad groups: the earlier runs of eastern Kamchatka which reach their streams in June or early July and the later runs of western Kamchatka which reach their streams in the latter half of July and in August.

Timing of the runs to North American streams seems more complex.[3] The peak of the migrations of sockeye salmon to Bristol Bay streams generally occurs in the first 2 weeks of July, although some numbers enter as early as June 15 or as late as August 15. The Chignik River fish first appear in late May, reach a maximum between June 10 and July 15, and continue to enter until late September. The run to the Karluk River begins in mid-May, lasts until mid-October, and has two peak periods. The first lasts from early June to July 1, and the second from late July to mid-September (Rounsefell, 1958). The catch in Cook Inlet is supported by several streams. The fish appear from late May until late August but are most abundant from mid-July to early August. The catch in Southeastern Alaska is supported by fish from many streams, most of which have small runs. Fish appear in early June, reach maximum numbers in late July and early August, and are scarce after early September. The Skeena River sockeye arrive from late June until mid-August, and the run peaks between July 15 and August 1. The peaks of the Fraser River runs are most variable. Because the tributary systems have their own unique races, the characteristics of the peaks in a particular year depend upon which races are dominant in that year. Several peaks occur within a year as each major race approaches the river. Sockeye enter the Fraser River from early July until late September, and the dominant peak usually occurs between the latter part of July and early September.

The variation in the times when sockeye salmon reach their spawning streams is evident (fig. 2). Fish begin to arrive in large numbers in the Karluk River as early as June 1, and may continue to arrive in large numbers in the Fraser and Karluk Rivers until mid-September. With the exception of these rivers, the duration of heavy migration tends to be shorter, occurring within 6 weeks, and generally lasting less than a month for the major runs. These differences in timing must have a pronounced effect upon the distribution of maturing sockeye salmon in the sea. After the middle of July, for example, one would not expect to find in the sea any large part of the mature fish destined for the Kamchatka River or Bristol Bay rivers. If the speed of fish migration is considered with the time of their arrival at a particular stream, it should be possible to define areas of the sea which,

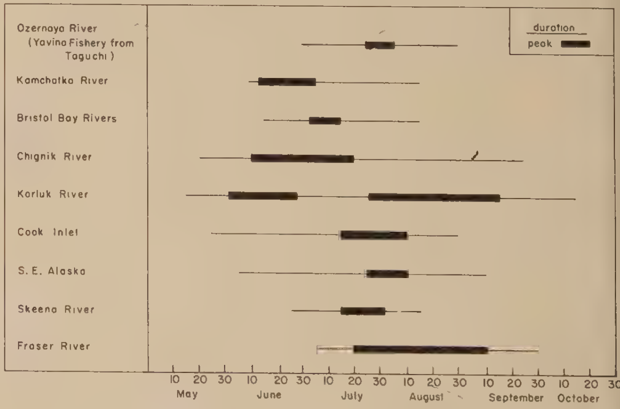

FIGURE 2.—Timing and duration of sockeye salmon migrations.

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[3] International North Pacific Fisheries Commission, Proceedings of the Seventh Annual Meeting, 1960, Vancouver, B.C. (INPFC Doc. 432) March 1961, 284 pp. [Processed.]

after a given date, would not contain maturing sockeye salmon from that stream. This feature may determine the origin of some groups of fish found on the high seas.

HIGH SEAS DISTRIBUTION

While the data related to the high seas distribution of salmon have not yet been analyzed thoroughly, there is information available from partial analyses and from the catch records of research vessels of Canada, Japan, and the United States, as well as from the Japanese high seas mothership fisheries. The data are deficient in two respects: First, almost all of the fishing has been done between May 1 and September 30, and second, comparable areas have not been fished each year.

SURFACE

Fishing with surface gill nets has shown that sockeye salmon are widely distributed in the North Pacific Ocean and Bering Sea from North America to Asia. Sockeye salmon have been caught in May as far south as lat. 45° N. in the western Pacific Ocean, and as far south as lat. 47° N. in the eastern Pacific Ocean (Bureau of Commercial Fisheries chartered research vessel *Bertha Ann*, March 1962). In June they have been caught at lat. 62° N. in the Bering Sea.[4] It is likely that the ocean range of the species exceeds these boundaries; indeed they are regularly found, at least in restricted localities, outside of these latitudes. Every year they enter the Columbia River (lat. 46° N.) and the Noatak River [5] (lat. 62° N.).

Little is known of the oceanic distribution of sockeye salmon from October through April. If, as has been commonly assumed, the fish at sea move southward in the winter, the area in which they are found in May might be taken to approximate that occupied during the preceding winter. During May, 1956, three Japanese vessels, *Eiko Maru*, *Takuyo Maru*, and *Etsuzan Maru*, explored an area bounded roughly by long. 160° E. to 175° W. and from lat. 40° N. to 50° N.[6] The southern limit to which sockeye (maturity not stated) were found is shown in figure 3. The

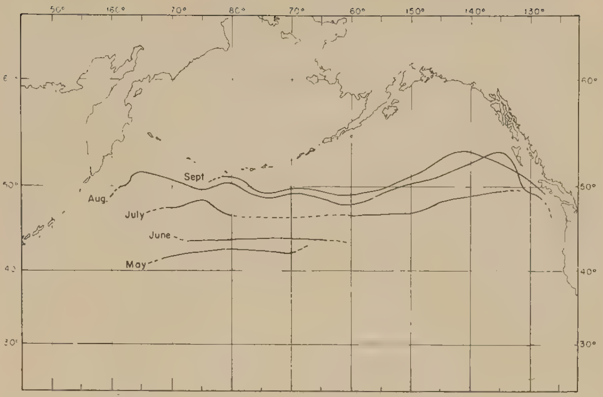

FIGURE 3.—Southern limits of sockeye salmon see footnote 7.

northern boundary of sockeye salmon between long. 175° E. and 180° appeared to be near lat. 50° N. The evidence indicates that by late May 1956, sockeye salmon had not moved as far north as the Aleutian Chain. This supposition is supported by the distribution of the Japanese high seas fishery which takes place well south of the Aleutian Islands in May. However, the supposition that the salmon all move south in winter, is contradicted by the catches of the Bureau's research vessel *Bertha Ann*. She caught considerable numbers of sockeye salmon as far north as lat. 51° N. at long. 175° W. in February 1962, and lat. 57°28′ N. at long. 175° E. in February 1963. Fishing was not done further north.

The seasonal changes in the north to south distribution are poorly understood; however, figure 3 clearly shows a northerly displacement of oceanic sockeye salmon in successive months from May to September 1956.[7]

The distribution of the maturing salmon and the immature fish must be somewhat different because of their different requirements. As the spawning time approaches, the maturing fish must migrate to their streams to reproduce. To flourish, immatures must be distributed in whatever manner best suits survival and growth. The distribution of maturing and immature salmon should be considered separately for these reasons. Favorite [8] in figures 23 and 24 (also INPFC, 1960, p. 91) shows a persistent decline in the size of sockeye salmon as fishing proceeded in a southerly direction. This is indicative of increasing percentages of immature salmon to the south. We have reason to believe from the results of high seas fishing that sometime during the winter the immature sockeye retreat to the south in the middle and western parts of the northern Pacific Ocean. Although information for the Gulf of Alaska is meager, Manzer's data for that area also suggest a southward retreat in winter. Data on the winter distribution of sockeye salmon are almost totally lacking. With the onset of maturation the maturing individuals separate from (if they were mixed) the immature elements of the stocks.

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[4] Kasahara, H., and L. M. Kissack, Statistical Yearbook 1960, International North Pacific Fisheries Commission, Vancouver, B.C., 1961, pp. 1–67.

[5] Reported by Clifford H. Fiscus, U.S. Fish and Wildlife Service, Seattle, report of 1955 field activities.

[6] Konda, Mitsuo, Distribution area of salmon in the High Seas, Suisan chō (Fisheries Agency of Japan). In two parts—(INPFC Doc. 309 (1) and 309(2)). [Part I—English summary, 10 pp.; part II—Japanese text 8 pp. and 22 pp. in English.]

[7] Manzer, J. I., Salmon Distribution and Abundance in the northeast Pacific, 1956–57, Fisheries Research Board of Canada, Nanaimo, B.C. (INPFC Doc. 195), 1958, 8 p. [Processed].

[8] Favorite, Felix, Progress Report of Oceanography, Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 319), 1959, 8 pp. [Processed.]

The research vessels in the Aleutian Region in June catch principally maturing fish (Hartt, 1962; and Margolis, 1963.) The maturing fish continue to be relatively abundant in the central and eastern Bering Sea, and along the Aleutian Islands until late June. Off southeast Kamchatka their abundance decreases in July and they become comparatively rare by August.

The distribution of maturing sockeye salmon in the Gulf of Alaska is less well known. Experimental catches have not been as large as in the Aleutian area. Maturing fish have been taken throughout the region north of lat. 50° N. and east of long. 150° W. (INPFC, 1957), between May and July. Intermittent fishing has shown them to be present at sea south of the Alaska Peninsula.

The maturing sockeye precede the immature fish in the more northern waters. In late May or early June the immature sockeye salmon appear to be situated south of the maturing individuals in the Aleutian Islands area (Hanavan, 1961). In the western Gulf of Alaska (south of Kodiak Island and the Alaskan Peninsula), immature salmon are found in fair abundance. In late June immature sockeye begin to replace the maturing fish in the catches off east Kamchatka and near the Aleutian Islands. By July immature fish are generally dominant from southeast Kamchatka along the Aleutians and well into the Gulf of Alaska. In August the fish are chiefly immature in the catches along the east coast of Kamchatka (Ishida and Miyaguchi, 1958). This is also true in the Aleutian Islands area, in the Bering Sea, and in the western Gulf of Alaska.

SUBSURFACE

The ocean distribution described above has been determined by surface fishing, however, the subsurface distribution may be different. Relatively little is known of the sockeye salmon in the deeper layers of the sea. Fishing in the Gulf of Alaska [9] demonstrated that in the absence of a thermocline, this species is found to depths of at least 200 feet. A seasonal change in depth distribution in the Gulf of Alaska may be associated with the development of the thermocline. During summer when a marked thermocline existed, the fish were caught only in the layer above the thermocline. The depth distribution of maturing and immature sockeye salmon appeared to be about the same.[10] It is not known whether the same vertical distribution pattern occurs elsewhere. The experiments indicated that salmon made diurnal migrations and were most abundant near the surface at night. This may explain the pattern of the Japanese mothership fishery in which the catch is taken at night with surface nets.

MIGRATION

Sockeye salmon are caught across the North Pacific Ocean and Bering Sea; consequently, some of them must migrate at least to midocean at the latitudes in which they are found. Because immature fish are believed to be scarce or absent in the Bering Sea in the colder months and from the southern part of their ocean range in the warmer months, they probably undertake considerable migrations in a north-south direction.

There are several possible methods of studying the migrations of sockeye salmon in offshore waters. First we will consider what can be discovered of the migrations from fishing indices.

Analysis of high seas catches of sockeye salmon could probably identify migration of major groups of salmon. Differences in numbers of fish, their size, sexual development, age, and timing of migration might be used to trace movement. Analysis of research vessel data, however, has not been completed, and detailed data needed from the mothership fisheries are not generally available.

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[9] Manzer, J. I., and R. J. LeBrasseur, Further Observations on Vertical Distribution of Salmon in the Northeast Pacific, Fisheries Research Board of Canada, Nanaimo, B.C. (INPFC Doc. 311), 1959, 9 p. [Processed.]

[10] Neave, Ferris, Observations of the Vertical Distribution of Salmon in Northeast Pacific, 1960, Fisheries Research Board, Canada (INPFC Doc. 408), October 1960, 5 p. [Processed.]

Two interesting papers on migration are those by Johnsen[11] (1962) and Hartt (1962). Johnsen examined data on the direction from which salmon entered the gill nets fished by U.S. research vessels in 1959 and 1960. These data are grouped by May–June and by July–August catches (figs. 4 and 5). The May–June catches are predominantly maturing fish, and the July–August catches predominantly immature sockeye salmon. (The movement of fish is shown as being perpendicular to the axis of the gill net on each set.) Caution must be used in interpreting these figures. Where direction of migration is shown by an arrow, fish could have approached the net from somewhat different directions, but if they entered the net from the same side, the differences would not be detected. The situation where fish are shown to be moving about equally in opposite directions could also arise if the fish were caught while moving in a general direction more or less parallel to the net. Therefore, we must question the instances in which fish are shown to be moving equally in opposite directions, and consider that where movement is shown to be predominantly in one direction, the direction shown is not precise.

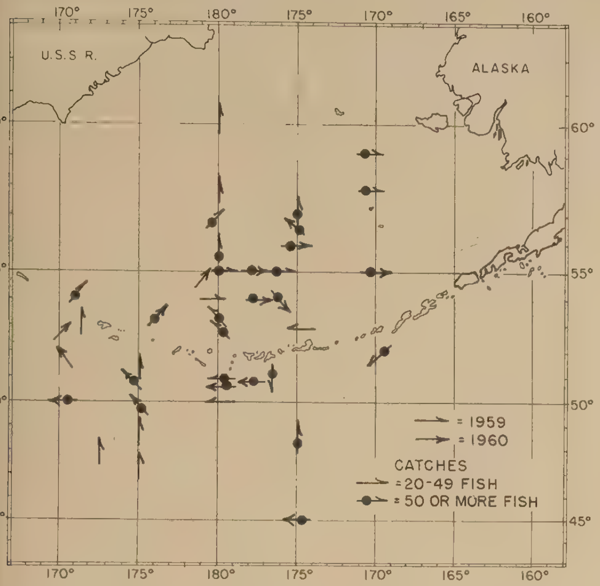

FIGURE 4.—Dominant direction of movement of red salmon indicated from gill net catches during May and June 1959 and 1960.

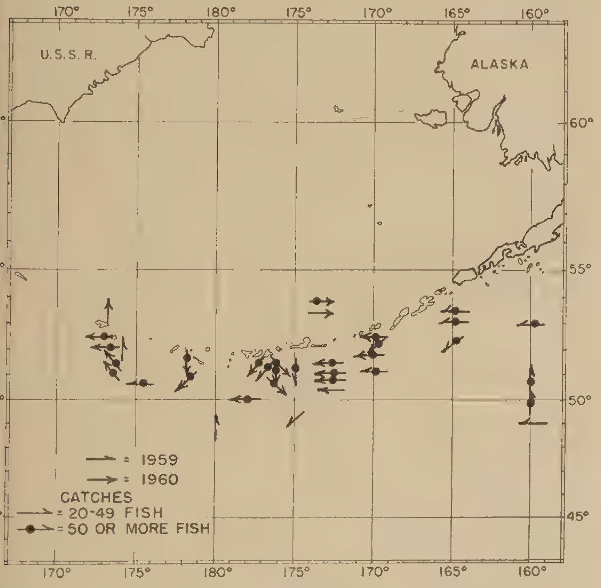

FIGURE 5.—Dominant direction of movement of red salmon indicated from gill net catches during July and August 1959 and 1960.

For maturing fish (fig. 4) the direction of movement in the North Pacific Ocean was westward as far west as long. 180°. At long. 175° E. the migration was north or west. Near long. 170° E. it was west, northwest, north, and northeast. In the Bering Sea, movement was generally in a northerly or easterly direction, although there are some marked exceptions at long. 180° and 175° W.

Immature fish in July and August (fig. 5) showed northerly or westerly movement in the western Gulf of Alaska and westerly movement in the North Pacific Ocean to long. 173° W. Between long. 175° W. and 175° E. the direction of movement was confused. Between long. 175° and 170° E. the direction again became strongly north and west. Too few catches of immature sockeye salmon are shown in the Bering Sea to provide an indication of the pattern of movement.

Hartt (1962) used the direction in which purse seine nets were set to study the direction in which sockeye salmon were migrating in the ocean. He pointed out that for the seine to catch fish in the manner it did, the fish must have been actively moving through the water. The purse seine is set to catch fish approaching from only one side of the net. By comparing the numbers caught when the net was set in opposite directions, the relative directional movement was revealed.

In the North Pacific Ocean he found that the catches "clearly illustrate the pronounced westward movement along the south side of the Aleutians for both mature and immature reds (sockeye) as far as 175° East longitude . . . opposed movement to be only slight or lacking. West of 175° East longitude, movement becomes more mixed, but westward movement is still pronounced. Northward movement through Amchitka and Buldir Passes is indicated positively only later in the season when immatures were present. In the Bering Sea, the eastward route near the Pribilofs is shown between June 16 and 30."

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[11] Johnsen, Richard C., Directional Movement of Salmon in North Pacific Ocean and Bering Sea as indicated by Surface Gill Net Catches, 1959-60, Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 569), 1962, 65 pp.

These two sources indicate that from May through August, both the mature and immature sockeye salmon found in the North Pacific Ocean show a strong westward (and presumably northward) migration from long. 165° W. to 170° E. Although Hartt's observations were for the years 1956, 1957, and 1958 and Johnsen's were for 1959 and 1960, the results are quite similar. From the Bering Sea observations, the movement of maturing sockeye seemed to be mainly to the north and east. No observations were available with reference to movement in the Gulf of Alaska or in waters west of long. 170° E.

ENVIRONMENT

The migrations of sockeye in the sea, particularly during the homeward migration, seem to be related to the hydrography of the North Pacific Ocean and the Bering Sea. Taguchi (1957b) showed that the distribution of salmon in the Pacific Ocean west of long. 180° coincides with that of the dichothermal water which shows Oyashio (cold) water, and that the southern boundary of the distribution lies along the belt where the Kuroshio encounters Oyashio water. Taguchi (1957a) further stated that the oceanic migration of salmon coincides with the movement of water and that the best catches (presumably reflecting greatest abundance) will be made where a tongue of cold water intrudes into a branch of the Kuroshio.

Work by Favorite (INPFC, 1958) clearly shows that adult sockeye salmon which were going to Bristol Bay, Alaska, were moving along and quite close to the body of cold water (less than 3° C. from surface to bottom) near lat. 57° N. and long. 170° W.

In the central North Pacific Ocean, in the region where salmon are found, the movement of water is easterly, except for the narrow return flow south of the Aleutian Islands. If the ocean migration of maturing fish were always with the prevailing current, the sockeye salmon should be moving easterly in the central regions when beyond the influence of the west current immediately south of the Aleutian Islands. Available evidence (figs. 4 and 5) indicates that this is not true; therefore, factors other than current direction may influence the direction of migration.

It is certain that the ocean environment strongly affects the distribution of salmon on the high seas. Favorite and Hanavan [12] showed that the southern limit of salmon as determined by surface gill net catches may be more directly related to subsurface than to surface conditions. Favorite [13] and INPFC (1958) showed good correlation between the surface distribution of salmon and temperature at depth. During fishing operations along long. 155° W., surface temperature varied little. When the subsurface temperature minimum was no longer present, however, no salmon were caught at the surface. Although the temperature at the surface was about the same, sockeye salmon did not occur over the area which had warmer subsurface temperatures. For these reasons we might conclude that temperature may be only an indicator of the water inhabited by sockeye salmon, and not a precise limiting factor.

Konda [14] stated that sockeye salmon were caught in surface nets when water temperatures ranged from 4.3° to 6.9° C. and that they were most abundant between 5° and 6.9° C. Manzer,[15] however, reported that they were caught in the Gulf of Alaska at temperatures from 7° to 15.9° C. Fish seemed most abundant between 7° and 11.9° C. in 1956 and between 9° and 13.9° C. in 1957. These variations suggest that at surface water temperatures between 4° and 16° C., factors other than temperature may control the distribution of sockeye salmon.

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[12] Favorite, Felix, and Mitchell G. Hanavan, Oceanographic condition and salmon distribution south of Alaskan Peninsula and Aleutian Islands 1956, Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 415), 1960, 34 p.

[13] Favorite, Felix, Progress report on oceanography, Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 152), September 1957, 8 p. [Processed].

[14] Kondo, Heihachi, Progress report on tagging experiments conducted in 1961 and additional recovery information for 1960 tagging, in Japanese (English translation by INPFC Secretariat, INPFC Doc. 485), October 1961, 3 p.

[15] Cited by Manzer in footnote 7, p. 451.

It is possible that the oceanic environment in which maturing sockeye salmon are found might not be particularly favorable. The migration to their natal stream might take them into environments that are unfavorable, but which are tolerated in order to reach the spawning grounds. Thus, the circumstances in which the maturing fish are found may not represent optimal conditions, but merely an area through which they must pass.

In summary, the sockeye salmon inhabit a band of ocean reaching from Asia to North America. The position and perhaps the width and density of this band shifts with seasonal changes in the environment. In fall the fish seem to retreat from the Bering Sea and Aleutian Islands area. In late spring and summer, they reappear. It is most likely that features of the environment, such as food supplies and temperature strongly influence this distribution. Because the characteristics of the Gulf of Alaska are less affected by seasonal changes than the sea near Kamchatka, it seems likely that the displacement of sockeye salmon would be less marked. The shift is nevertheless apparent, but the fish apparently do not move as far southward. The distribution of these fish in the high seas is continually changing. Maturing fish are found over wide areas of the sea in early summer and disappear when they migrate to their streams. Immature fish (fish which are not going to mature within the calendar year of capture) are usually scarce at sea near the Aleutian Islands while maturing sockeye salmon are present; by July immature fish are abundant in this area.

Seasonal distribution combined with spawning time and location of spawning ground determines to some extent the direction of homeward migration. If the fish are south of lat. 50° in May in the central Pacific Ocean their spawning migration would probably have a northerly directional component because most of the major spawning streams lie north of this latitude. This would also be the case for Bristol Bay fish in the Gulf of Alaska, but not for Fraser River fish. Fish which begin a spawning migration in June would probably tend to go more directly east or west.

We can now reconstruct partially the oceanic migrations of sockeye salmon. Their movements are obscure after they leave the river mouth until they begin their second summer in the sea. In June of their second summer at sea, sockeye salmon are found to be moving northward. This situation persists through the summer. From both fishing observations and tagging results, there appears to be a strong movement of immature fish to the westward along the south side of the Aleutian Islands. In the region of the Commander Islands movement seems to be predominantly to the north. This movement should shift the abundance of fish to the west and north. It is not clear if an individual fish will travel, for example, from the eastern end of the Aleutian Islands to the Commander Islands and northern Kamchatka. More extensive study of the migrations of immature salmon is needed.

After the end of summer the young salmon evidently migrate south to spend their second winter in the sea. The following spring we again find them distributed across the ocean and engaged in a general northward movement. This might not be so marked in the Gulf of Alaska as it is farther west. Migration south of the Aleutian Islands (and to some extent further east) is predominantly westward. Maturing fish which have spent two summers and winters at sea precede those which have been at sea equally long but which are not maturing.

From the tagging results which are discussed later it seems that maturing sockeye salmon destined for Kamchatkan streams continue to move west, but that the Bristol Bay fish go west for a distance, turn north through one of the passes into the Bering Sea, and proceed north and east to Bristol Bay. Evidently, most of the maturing fish south of the Aleutian Islands migrate westward regardless of whether their final destination lies to the east or west. Fishing provides no evidence that any substantial eastward movement by maturing fish exists south of the Aleutian Islands. Some exceptions to this must be in fish that are traveling to the Chignik River, Kodiak Island, or the British Columbia coast. Presumably, sockeye salmon that were going to Kamchatka from the Aleutians area would migrate west and then either north or south to reach the east or west coast of Kamchatka.

All sockeye salmon do not mature after their second winter in the ocean. These immature "two winter" fish, which are nearly as large as those which matured, apparently behave in the manner described for them as immatures a year earlier.

ORIGIN OF SOCKEYE SALMON IN OFFSHORE WATERS

From the preceding discussion it is evident that sockeye salmon travel far during their ocean existence. They are widely distributed on the high seas, and fish from rivers of both Asia and North America may be found in approximately the same part of the sea simultaneously. We then may consider origins of stocks caught on the high seas, and also, where they are of more than one origin, the relative proportion of each. This problem is complicated by the constantly changing distribution. Evidence now available indicates that before June there may be relatively few maturing salmon in the Pacific Ocean near the Aleutian Islands or in the southern Bering Sea. By the end of June large numbers of fish have entered these waters, traveled through them to various destinations, and have disappeared. Thus it is plain that to speak precisely of quantities of fish from each of several different streams is difficult. The numbers and destinations of fish in any area are apt to be changing. Further, as shown earlier, by far the greater numbers of salmon originate in a relatively few streams. It is almost impossible to discover and trace the very small groups that inhabit some of the streams along the Pacific Ocean rim. There are many streams each of which has a total run of only about one thousand salmon.

Although some information is available from other sources, knowledge of the origin of sockeye salmon on the high seas is principally from earlier work by Japanese scientists or from studies made by Canada, Japan, and the United States for the International North Pacific Fisheries Commission. This origin problem has been studied using tagging, scales, distinctive parasites, serology, and morphology. These studies have dealt separately with maturing and immature sockeye because of the marked difference in their distribution and movements. The work with maturing fish has progressed more rapidly than that with immature fish.

TAGGING STUDIES

The results of tagging experiments add enormously to our knowledge of the origins of sockeye salmon in the high seas.

Japanese scientists have studied oceanic migrations of sockeye salmon over a period of years. From the results of tagging, Sato (1938, 1939) determined that the sockeye salmon offshore of southeast Kamchatka went north to the Kamchatka Gulf in May and south to the west coast of Kamchatka later in the year. He presents a schematic chart which shows sockeye salmon proceeding westward from the area south of Attu Island (ca. long. 173° E.) to the coast of Kamchatka and then proceeding north and south. He estimated that the average speed of travel of sockeye salmon at sea was 12.5 miles per day for mature fish traveling from Cape Kronotski (southeast Kamchatka) to the Ozernaya River in west Kamchatka.

Taguchi and Nishikawa (1954) gave a more detailed review of the movements of sockeye salmon in the western Pacific Ocean. The description they gave corroborates and extends the earlier work. They found fish traveling from the oceanic area southeast of the Kamchatka Peninsula north to the Kamchatka River and minor streams beyond, or south and west to the streams on the west coast of the Kamchatka Peninsula. They gave 3.3 to 9.3 miles per day as the average speed for directional movements along the west coast of Kamchatka.

In 1958, 1959, 1960, and 1961 (Japan Fishery Agency, 1959, 1960, 1961, and 1963) Japanese scientists conducted extensive high seas tagging experiments (fig. 6). The discussion here is limited to returns within the year of tagging in an effort to eliminate immature fish from consideration, but some of those taken by the high seas fishery might have been immature. The reports are not clear on this point. Most fish were released in June; some were tagged in July near Kamchatka in 1958. Some of the sockeye salmon tagged north of lat. 50° N. and west of about long. 165° E. were recovered in Asia. No American recoveries were made of fish tagged in this area. According to Sato (1939), the maturing fish from this area went to both east and west Kamchatka.

Recoveries in North America are shown for the sockeye salmon tagged north of about lat. 50° N. and east of about long. 170° E. in the North Pacific Ocean and Bering Sea. The one inshore recovery from tagging in the Bering Sea west of long. 180° was from Bristol Bay. No Asian recoveries resulted from tagging in these areas. The inshore recoveries were made mostly in Bristol Bay, Alaska, from tagging in both the

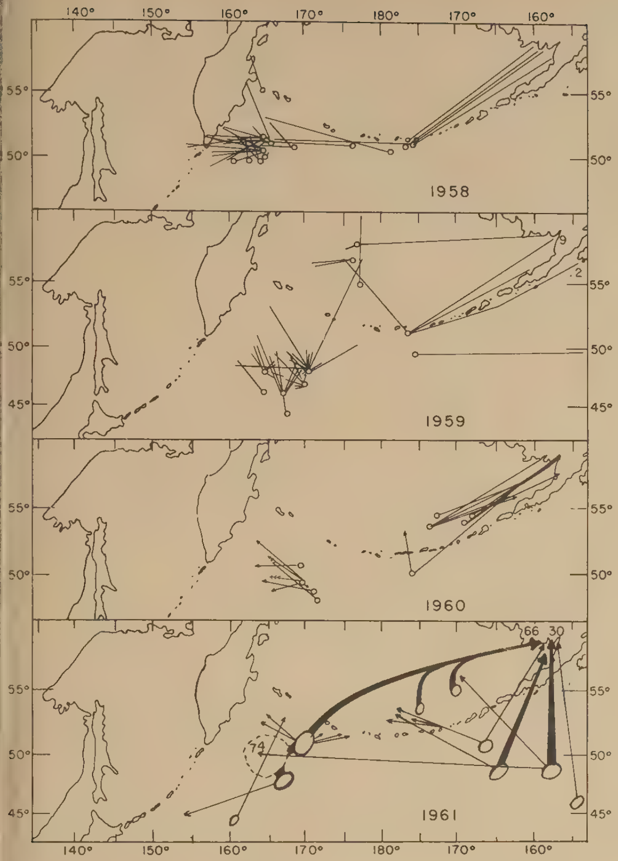

FIGURE 6.—Ocean migrations of sockeye salmon as shown by Japanese tagging experiments in 1958, 1959, 1960, and 1961.

North Pacific Ocean and in the Bering Sea. In 1959, however, there were two recoveries at Kodiak Island, Alaska, and one at Somerville Island, British Columbia, from fish tagged in the North Pacific Ocean between long. 175° W. and 180°.

In 1961, Japanese tagging[16] was more extensive in time and area. Tagged sockeye salmon were released from about long. 160° E. to about 155° W. and from south of lat. 45° N. to near 55° N. (fig. 6). The releases in the Gulf of Alaska were made between late April and late May, and those shown for the western Pacific Ocean were made from mid-May to early August. The inshore recoveries greatly strengthen our knowledge of the sea distribution of maturing sockeye salmon from several areas. There were returns to Bristol Bay from fish released near lat. 50° N. between about long. 165° E. and 170° E. and between long. 170° W. and 155° W. Fish from southeastern Alaska and British Columbia also inhabited the latter area. Two recoveries were made in southeastern Alaska and one at Rivers Inlet, British Columbia.

Canadian tagging in the Gulf of Alaska (INPFC, 1963) provides a much clearer understanding of the origins of maturing sockeye salmon in the region south of Kodiak Island than previously existed. Fish from Western, Central, and Southeastern Alaska and from British Columbia were represented in the area roughly bounded by lat. 54° N. to 58° N. and long. 148° W. to 154° W. (fig. 7). Tagging was done mainly in June and July.

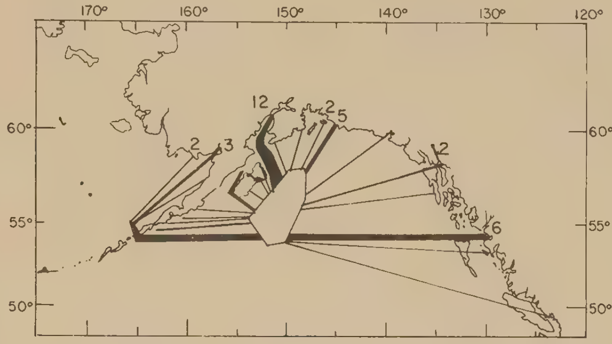

FIGURE 7.—Recovery distribution of sockeye salmon 1961.

The U.S. Section of the International North Pacific Fisheries Commission has sponsored high seas salmon tagging since 1955. The results are summarized in the Annual Reports of the Commission for the years 1956 through 1961. The experiments were conducted by the Fisheries Research Institute of the University of Washington under contracts with the Bureau of Commercial Fisheries. Figure 8 shows the results of tagging maturing (mostly in late May and in June) sockeye salmon in 1957, 1958, and 1959. The results for 1956–58 are reported in detail by Hartt (1962). The 1956, 1960, and 1961 experiments, which are not shown, emphasize the dominance of Bristol Bay recoveries of maturing sockeye salmon tagged near the Aleutian Islands east of long. 175° E. These years are not shown here because they are quite similar to 1957–59.

There were no recoveries in Asia of maturing sockeye salmon from the U.S. tagging experiments of 1955 to 1961. American inshore recoveries were obtained from sockeye salmon tagged in the North Pacific Ocean as far west as long. 173° E.,

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[16] See footnote 14, p. 454.

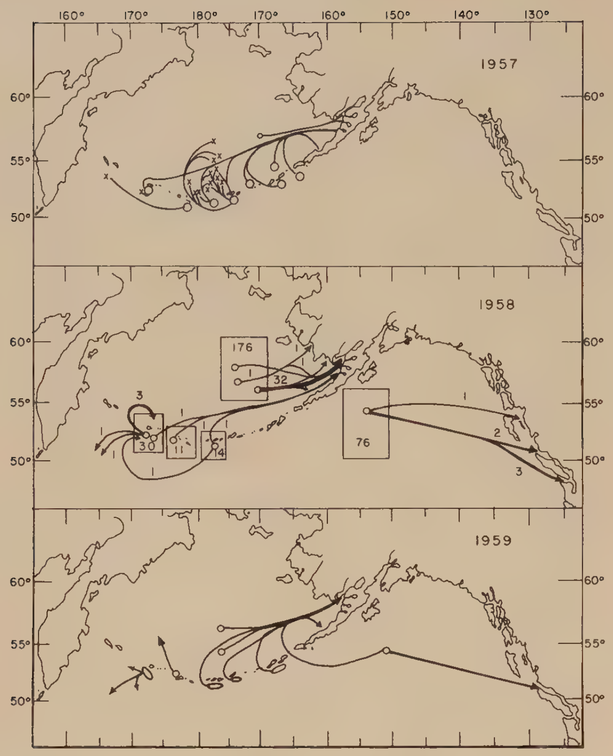

FIGURE 8.—Ocean migrations of sockeye salmon tagged by United States (INPFC, 1958, 1959, 1960c).

and in the Bering Sea nearly as far west as long. 180°. Again, nearly all of the inshore returns were from Bristol Bay, Alaska. There were also recoveries from other areas: one in Chignik River (1956) and one in Cook Inlet (1961) from fish tagged in the North Pacific Ocean near long. 165° W. (not shown), a recovery in the Kuskokwim River of a fish tagged in the Bering Sea near long. 175° W. and seven recoveries on the British Columbia coast of fish tagged between long. 150° W. and 155° W. south of Kodiak Island. Most of the seven were probably destined from the Fraser River. Fish that were released closer to Kodiak Island in 1961 had a different migration pattern (Hartt, 1963) and were recaptured from only Western and Central Alaska. Fish tagged near lat. 56° N. and long. 140° W. were recovered from Southeastern Alaska and northern British Columbia.

Hirano and Kondo[17] reviewed the results of high seas tagging by Japan and the United States. They examined the recoveries of mature sockeye salmon according to the month of tagging. Most of the fish, however, were tagged in June. The May experiments were small, and in July the mature fish were no longer caught in the high seas areas. Their discussion of maturing sockeye salmon is primarily concerned with the distribution of the Bristol Bay fish. They express the opinion that from late May to June red salmon of Bristol Bay origin are distributed in the Bering Sea east of the line drawn between Attu Island and the Yukon River as well as along the Aleution Islands, and that the Bristol Bay fish mix with red salmon originating from the Asian continent in the waters around Attu to Adak Island in May and June. Hirano and Kondo suggest that the direction of migration shown by tagged fish retaken on the high seas indicates that some sockeye of Asian origin also occurred south of the Aleutian Islands west of Adak Island.

Tagging recoveries show the eastward extent of migration for maturing Asian salmon and the westward extent for maturing North American salmon (figs. 9 and 10). The results of all of the sockeye salmon tagging experiments discussed earlier were employed in constructing these figures. In figure 9 the seaward limits of Asian and North American sockeye salmon are shown to the extent that they have been proved by recoveries in the home streams. Recoveries of tagged maturing sockeye salmon have been made in Asian streams from tagging in the North Pacific Ocean as far east as about long. 175° E. (Hirano, 1953). Although tagged fish have been released in the Bering Sea, none have been recovered in Asia. Tagged fish

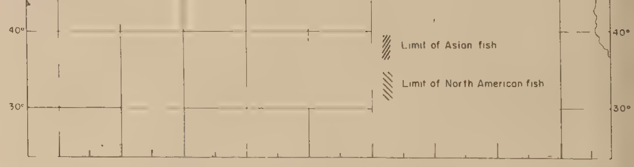

FIGURE 9.—Seaward limits of maturing sockeye salmon migration as shown by tag recoveries in or near spawning streams.

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[17] Hirano, Yoshimi, and Heihachi Kondo, Salmon Tagging experiments in high seas of North Pacific, Fisheries Agency, Japan (INPFC Doc. 324), September 1959, 10 pp.

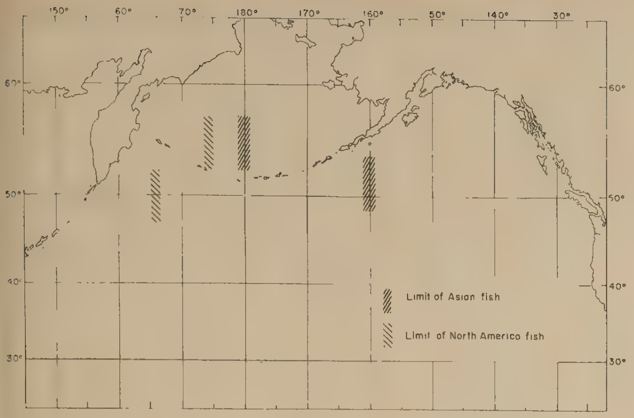

FIGURE 10.—Seaward limits of maturing sockeye salmon as inferred from direction of movement by salmon recovered on high seas.

have returned to North American streams from tagging operations near long. 167° E. in the North Pacific Ocean and from operations near long. 175° E. in the Bering Sea.

The recoveries shown in the figures are maturing salmon except where noted. If we assume that the ultimate destination can be inferred from the direction in which the fish traveled prior to capture, it is possible to speculate on the migrations which some of the fish captured on the high seas were undertaking (fig. 10). On this basis, maturing Asian fish appear to be migrating homeward from as far east as long. 159° W. in the North Pacific Ocean and from long. 179° W. in the Bering Sea. American fish appear to be migrating homeward from as far west as about long. 165° E. in the North Pacific Ocean and from about long. 175° E. in the Bering Sea. These limits can perhaps be useful in examining the extreme distances at which maturing Asian and North American fish might be found.

The procedure used in figure 10 is of doubtful validity. It is not known for certain that all of the high seas recoveries were maturing fish enroute to their spawning stream. In some instances they probably were immature fish of unknown origin engaged in a feeding migration. Further, the maturing fish enroute to the rivers generally move westward along the south side of the Aleutian Islands even when their ultimate destination is in Bristol Bay, which lies to the eastward. For these reasons we must conclude that we are unable to identify with any certainty the ultimate destination of a tagged fish recovered on the high seas.

The movements of immature sockeye salmon in the ocean are less clear than those of maturing sockeye. High seas recoveries of salmon tagged as immatures usually cannot be assigned to any final destination. Most were tagged during one summer season and recovered a year later. Because the intervening movements could have been and probably were extensive, it is difficult to place significance on distance between release and recovery points. With the exception of one that was released near lat. 52° N. and long. 172° E. and recovered in Kamchatka Bay, stream recoveries of salmon tagged as immatures were obtained only from North America. These again are chiefly from Bristol Bay, Alaska, and from fish tagged in the preceding summer at sea in the waters immediately south of the Aleutian Islands between long. 167° W. and 173° E. In addition, one fish tagged when immature at long. 177° E. was recovered at Rivers Inlet, British Columbia; another that was tagged south of Kodiak Island at long. 156° W. was caught at the mouth of the Fraser River, British Columbia.

From the discussion of high seas migrations it is clear that in the North Pacific Ocean maturing Kamchatkan sockeye salmon have been found in June as far east as long. 175° E. Maturing sockeye salmon tagged as far west as long. 167° E. and as far east as long. 150° W. have been recovered in Bristol Bay. Sockeye salmon tagged as far west as long. 177° E. in the Bering Sea in June were recovered in Bristol Bay.

Most of the maturing sockeye salmon tagged south (fig. 8) of the Aleutian Islands as far west as long. 175° E. appear to have been migrating westward when caught and tagged. Recoveries were mainly from Bristol Bay or the Bering Sea east of long. 180°. Although there are certain exceptions, tagged fish released near the south side of the Aleutian Islands usually did not proceed as much as 10 degrees of longitude further westward. However, those shown in figure 6 migrated from near long. 160° W. to almost 180°, and showed a distinct northward movement as well.[18] With one exception, they did not appear west of long. 180°. From the recoveries from these tagging experiments we infer that the maturing sockeye salmon found south of the Aleutian Islands are mainly of Bristol Bay origin.

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[18] See footnote 14, p. 454.

The fact that maturing Bristol Bay sockeye are intercepted by tagging vessels in a westward movement south of the Aleutian Islands when they are on a spawning migration to Bristol Bay, which lies to the east, makes it evident that these fish do not travel home by the shortest and most direct route. The work by Sato (1939) and Taguchi (1956) which was discussed shows that Asian sockeye salmon tend to travel first west, and then north or south when on their spawning migration to Kamchatka streams.

Early summer tagging has yielded some information concerning the origins of maturing sockeye salmon in the eastern Aleutian Islands area and in the Gulf of Alaska. Fish from Chignik, Kodiak Island, Cook Inlet, and northern British Columbia have been tagged in the North Pacific Ocean in the vicinity of long. 170° W. to 175° W. Sockeye returning to Kodiak Island, Cook Inlet, Copper River, Southeastern Alaska, northern British Columbia, and the important Fraser River have been tagged in the central Gulf of Alaska as shown by the preceding figures. While it is evident that the data are too few to describe the areas occupied by the runs to the streams of North America south of Bristol Bay, all of the runs seem to be represented in the region south of Kodiak Island.

The origin of immature salmon is poorly defined by tagging results. Examination of the tagging references considered earlier shows that immature fish which were probably Asian were tagged as far east as about long. 175° E. in the North Pacific Ocean. Immature North American (Bristol Bay) fish were tagged in the North Pacific Ocean as far west as long. 173° E. and in the Bering Sea as far west as long. 171° E.

From the tagging studies it is possible to reach certain conclusions concerning the origin of maturing sockeye salmon found in various areas of the North Pacific Ocean and Bering Sea.[19] Tag returns cannot be used to calculate precisely the percentages of fish of various origins in areas of the high seas unless it is known that inshore recovery rates are equal or can be adjusted. Little information is available on this point. However, Hartt (1962) pointed out that the complete lack of Asian returns is incompatible with the assumption that large numbers of maturing Asian sockeye salmon were present among his tagged fish. Considering these points with the tagging returns, it appears that most of the maturing sockeye found in June and July off the southeast coast of Kamchatka at least as far east as long. 170° E. were of Asian origin. Maturing sockeye salmon are found here in May, June, and the first half of July. In the tagging areas south of the Aleutian Islands where maturing fish are caught in late May and in June, the tagged fish were of Bristol Bay origin at least as far west as long. 175° W. in 1956, 1957, and 1958, long. 178° W. in 1959 and 1961, and long. 177° E. in 1960.

In the Bering Sea east of long. 177° W., virtually all of the sockeye salmon present along the north side of the Aleutians and in the Pribilof Islands area were of Bristol Bay origin. Although relatively fewer tags were released in the Bering Sea between long. 177° W. and long. 177° E., the only inshore recoveries were made in Bristol Bay, suggesting that Bristol Bay fish formed a majority of the maturing sockeye in this area. Maturing sockeye are found in the Bering Sea principally in June. From the Aleutian Islands eastward, less is known about the relative numbers of fish of various origins. Additional tagging is required.

MORPHOLOGICAL STUDIES

Differences in the morphological characteristics of North American and Asian sockeye salmon were used by Fukuhara, Murai, LaLanne, and Sribhibhadh (1962), Fukuhara (1961), and Landrum and Dark (1963) to determine the origin of sockeye salmon occurring in the Aleutian Islands area of the North Pacific Ocean and Bering Sea. In these studies, reference morphotypes or classificatory categories were chosen, certain morphological characters were selected to measure the racial differences between reference morphotypes, and a discriminant function analysis was employed to classify sockeye caught in the Aleutian Islands area.

Samples taken from the sockeye runs returning to Southwest Kamchatka and Bristol Bay-Chignik-Karluk River systems were chosen as reference morphotypes. These selections were based on evidence from tagging studies, parasite studies (which will be discussed later), and generalized distance function analyses (INPFC, 1958, 1959), all of which indicated that most of the maturing sockeye salmon in the Aleutian Islands area originated in Kamchatka or Western Alaska, and from information on the sizes of sockeye runs to various inshore areas, which showed that the Ozernaya River produced over three-fourths of the total Kamchatka catch while almost all Western Alaska sockeye originated in the rivers of Bristol Bay or Chignik and Karluk Rivers.

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[19] See footnote 14, p. 454, and INPFC 1963.

Seven morphological characters were used to measure the racial differences between the two reference morphotypes (scales in lateral line, vertebrae, caudal vertebrae, gill rakers, ventral gill rakers, pectoral fin rays and fin elements, and position of haemal arch). Each of these characters was carefully examined to make certain that no appreciable intra-morphotype variation was introduced by counting methods or differences in sex, age, life history, and time of sampling. The correlation between each character and fish length was determined to be negligible.

From samples obtained at sea off southwest Kamchatka and from streams in Western Alaska in 1956, the seven morphological characters were combined in a discriminant function. The amount of overlap between the two reference morphotypes was determined, rules of classification were established, and errors of misclassification were estimated. Since the Western Alaska reference morphotype was composed of several runs with differing errors of misclassification, it was necessary to obtain a weighted average error of misclassification for this morphotype. This was accomplished by weighting the error of misclassification for each run by its relative abundance as estimated from escapement counts.

Fukuhara et al. (1962) reported the classificatory results obtained by applying the discriminant function derived from the 1956 reference samples to high seas samples collected in 1956 and 1957. The authors also reported the details of the statistical analyses, tests of underlying assumptions, and empirical verification of the efficacy of the discriminant function. Classifications of the high seas samples taken in 1958 and 1959 and the development of confidence intervals for the classificatory results were discussed by Fukuhara (1961).

In each of the 4 years 1956–59 the samples taken in the Aleutian Islands area were divided into three groups: those taken in May and June; those taken in July; and those taken in August. The samples taken in May and June were composed mainly of maturing fish; the samples taken in July and August were mainly immature fish. Because the distributions of mature and immature sockeye were not the same, and underlying assumptions have not been satisfied for immature fish, the classification results were discussed separately.

Landrum and Dark (1963) used the discriminant functions derived from the 1956 reference samples to classify the 1960 collections. The average error of misclassification for Bristol Bay salmon was weighted by the relative abundance of the component stocks in the 1960 escapement.

The run to Bristol Bay in 1960 was very large (about 37 million according to Royce, 1961). We expected that the maturing sockeye salmon in large areas of the ocean, particularly in the Bering Sea east of long. 180° would be predominantly of Bristol Bay origin. As anticipated, all samples taken east of long. 175° E. in the Bering Sea were found to be chiefly of the Western Alaska morphotype. East of long. 180° the samples contained an estimated average of over 90 percent sockeye of Western Alaska morphotype. The upper 90 percent confidence limit averaged about 104 percent, and the lower limit averaged about 79 percent.

In the North Pacific Ocean in May and June 1960, maturing Bristol Bay sockeye salmon predominated in samples taken east of long. 180° with percentages ranging from 59 to 100 percent. West of long. 172° E. Kamchatkan sockeye salmon predominated by percentages ranging from 60 to 100 percent in samples that were mainly of maturing salmon.

Landrum and Dark further concluded that "the general trends in the east-west distribution of Kamchatkan and Bristol Bay stocks in both the Bering Sea and North Pacific Ocean are similar for the years 1956 through 1960."

A further matter of interest is the development of confidence limits for the point estimates of western Alaska type sockeye salmon (Fukuhara, 1961). The error caused by misclassification of fish was found to be a limiting factor in developing precise point estimates. For 1956 and 1957 (with errors of classification about 21 percent) samples of 150 to 200 fish had 90 percent confidence limits of about ± 8 percent. For 1959 (with an error of classification of about 30 percent) the 90 percent confidence limits were about ± 15 percent.

The origin of the maturing fish that were taken on the high seas seems best described by the summary given in Proceedings of the Seventh

Annual Meeting, International North Pacific Fisheries Commission.[20] In table 4 (taken from page 101 of that document) the percentages of Western Alaska morphotype in late May and June were averaged by 5-degree intervals of longitude for the North Pacific Ocean and for the Bering Sea according to year of sampling. These averages are shown in figure 11 and are referred to in 5-degree bands centered on the longitude indicated.

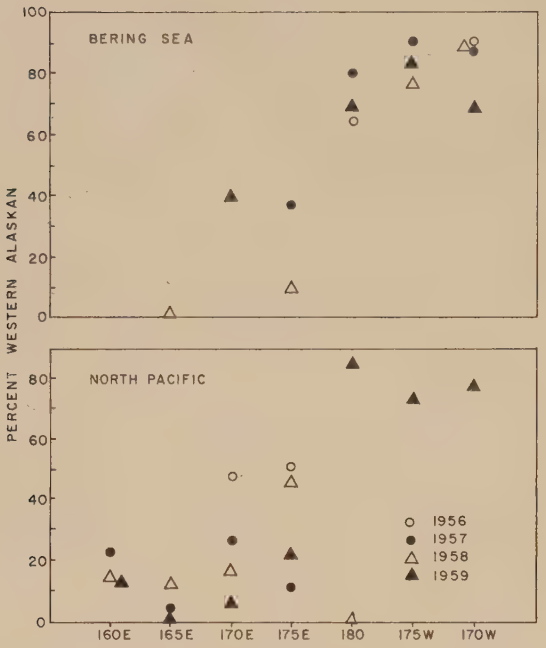

FIGURE 11.—Average percentages of Western Alaska morphotype in samples taken in the Bering Sea and North Pacific Ocean in late May and June 1956–59. (The 1958 sample at long. 180° was entirely of immature fish.)

These percentages show the following:

(1) In the Bering Sea, in the 180° band and eastward, the average percentage of Western Alaska morphotype in the samples ranged from 65 to 90 percent. Westward from this bank, the average percentages of Western Alaska morphotype in the samples decreased. In the 175° E. band and westward, the average percentage of southwest Kamchatka morphotype ranged from 61 to 100 percent. (2) In the North Pacific Ocean, from the Asian coast out to the 170° E. band, the average percentages of Western Alaska morphotype in the samples ranged from 0 to 40 percent. In the 175° E. band, the average percentages of Western Alaska morphotype ranged from 11 to 45 percent, except for 67 percent in 1956. In the 180° band and eastward, the average percentage of Western Alaska morphotype ranged from 72 to 85 percent in 1959, but in 1958 the single sample (taken in the 180° band) contained none of this type. (3) In the Bering Sea eastward from the 180° band and in the North Pacific westward from the 175° E. band, sampling from 1956 to 1959 was sufficiently intensive to suggest that the approximate ranges of percentages cited above reflect the relative proportions of the southwest Kamchatka and Western Alaska morphotypes present in these areas.

The morphological research cited above shows some interesting features of the high seas distribution of immature sockeye salmon in August. Because maturing sockeye are still present in the waters near Kamchatka and near spawning streams of North America in July, the samples in these areas may be either mature or immature. By August, maturing sockeye become relatively rare in the open ocean. As shown in the INPFC annual reports for the years 1959 and 1960 (INPFC, 1960, 1961) immature sockeye of the southwest Kamchatkan type appear to be distributed through the western Bering Sea as far east as long. 180.° They appear to be distributed as far east as long. 175° W. in the North Pacific Ocean and possibly as far east as long. 165° W. Because sockeye from British Columbia rivers inhabit this area, and the discriminant function incorrectly classifies most of such fish as south-

TABLE 4.—*Average percentages of Western Alaska morphotype in samples taken in the Bering Sea and North Pacific Ocean, late May and June, 1956–59* [1] [2] [3]

Location and year	Mid-points of 5° intervals						
	160° E	165° E	170° E	175° E	180°	175° W	170° W
Bering Sea:							
1956	--------	--------	--------	--------	65 (1)	-------- --------	90 (1)
1957	--------	--------	--------	36 (1)	80 (2)	90 (6)	87 (4)
1958	--------	0 (2)	-------- --------	9 (1)	-------- --------	78 (1)	89 (3)
1959	--------	--------	39 (3)	-------- --------	70 (10)	84 (6)	70 (3)
North Pacific Ocean:							
1956	--------	--------	48 (2)	51 (5)	-------- --------	-------- --------	-------- --------
1957	23 (1)	5 (3)	28 (4)	11 (3)	-------- --------	-------- --------	-------- --------
1958	15 (1)	12 (1)	18 (5)	45 (2)	0 (1)	-------- --------	-------- --------
1959	14 (3)	0 (2)	8 (10)	23 (5)	85 (2)	72 (4)	76 (2)

[1] The numbers of samples used for computing the averages are shown in parentheses.

[2] Taken from table 8, page 101 of (Proceedings of the seventh annual Meeting, 1960, International North Pacific Fisheries Commission, Vancouver B.C. INPFC Doc. 432, March 1961, 284 pp. (Processed).

[3] Deletion of samples containing more than 25 percent immature fish would eliminate the entries for the Bering Sea in 1957 at 175° E., and for the Pacific Ocean in 1957 at 175° E., and in 1958 at 180°. Deletion would also increase the average percentage in the Bering Sea 180° interval to 74 in 1956 and 78 in 1959. In the Pacific Ocean the average for 170° E. would change to 17 in 1958; in 1959, the averages become 10 for 170° E., 26 for 175° E. and 73 for 175° W.

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[20] See footnote 3, p 450.

west Kamchatkan morphotype, there is no way of determining whether the immature sockeye salmon of the western part of the Gulf of Alaska which are classified as Kamchatkan fish come from Kamchatka or from streams east of Kodiak Island.

Immature sockeye salmon of the Western Alaskan morphotype were found in August 1959 as far west as long. 170° E. in the Bering Sea. Indeed, a sample taken about 80 miles south of Cape Olyutorskii in 1959 showed strong evidence of immature Western Alaska type fish. In the North Pacific Ocean, Western Alaska type immature salmon were found from long. 160° W. to long. 175° E. Samples are lacking for the waters farther west. Landrum and Dark (1963) found that the Bristol Bay morphotype dominated all samples of immature sockeye salmon to long. 172° E. in July and August 1960. As in earlier years, the degree to which Bristol Bay fish dominated was not as pronounced in immature samples as in samples of maturing fish.

This may be the result of segregation of maturing fish into groups of common origin, or it could be caused by the presence of immature fish from areas other than Asia or Western Alaska. The analysis assumes that all fish are from these two sources. This assumption has been tenably justified for maturing salmon only. Although there is little evidence to negate the hypothesis for immature fish, there is a distinct possibility that sockeye salmon from North American streams other than those of Western Alaska may occur in the area. Analysis shows that the discriminant function used would misclassify these Kamchatkan salmon. A further but less serious error lies in the fact that the errors of misclassification for samples of immature salmon were not weighted in accordance to their abundance at maturity.

Analyses of the morphological characteristics of salmon east and south of Kodiak Island have not yet been reported. Preliminary studies have been made using the generalized distance function analysis with sockeye salmon data. This work is discussed briefly in the Annual Report for the year 1957 (also for 1958) of the International North Pacific Fisheries Commission (INPFC, 1958, 1959). This preliminary work using the distance function showed approximately the same distribution for Asian and North American sockeye salmon as was found by using the discriminant function.

SCALE STUDIES

Gilbert (1914–20) noted and described differences in scale patterns between races of Fraser River salmon on their spawning grounds. Various scientists since that time have used sockeye salmon scales in assigning fish of unknown origin to a particular spawning group. Scales of fish from different streams often have unique patterns. The use of scales for identification of the origin of sockeye salmon in the high seas is particularly attractive. When compared to alternate means of identifying high seas fish, scales are found to be relatively inexpensive to collect, store, and examine. Consequently, there has been a considerable amount of study designed to develop means of using scales to determine the origin of high seas sockeye salmon.

Although offering marked advantages over other means of identification, scale studies have difficulties that are not found in other methods. The usefulness of the scale method generally depends upon precisely counting or measuring various groups of circuli or areas of the scale. That scale reading has not yet developed into an exact science on a worldwide basis is evident. During the 1956 meeting of International North Pacific Fisheries Commission scale scientists, comparisons of age determinations were made on 436 sockeye salmon scales. Among a test panel of six scientists from Canada, Japan, and the United States, there was a disagreement of some sort concerning the total age of 55 percent of the test scales. This does not imply disagreement by all six on this percentage. Two scientists who had previously worked together disagreed on 11 percent between themselves, and their final conclusions disagreed by 4 percent from the ages considered to be correct. Relatively little difficulty was experienced with scales from Canadian fish; the disagreement was much greater for fish originating farther north. The range of disagreement for the six scientists was from 11 to 26 percent when compared with the age judged to be correct. There is no way at present of being certain that the ages judged to be correct really were. From subsequent tests it appeared that the difficulty lay chiefly in determining the number of annular marks in the fresh-water zone of the scale. This is of particular importance because most methods for identifying the origin of high seas sockeye salmon depend upon separating them into groups according to fresh-water life and total age.

The methods further require consistent measurement of the features employed to identify origin of the fish. Because scales are often very irregular in structure, exact criteria describing annuli are difficult to establish. Studies of the variation in number and spacing of circuli at various angles of the anterior field of the scales have not been formally reported, although experts commonly refer to this variation. There seems to be no published definition of the point at which measurements and counts start or stop for any particular study. Because of the lack of definitive descriptions of techniques and the lack of analyses of their reliability in general, it is nearly impossible to gauge the accuracy of the results unless some other means of measuring reliability is provided. Keeping the possible errors in mind, we can proceed to discuss the classification of high seas salmon to their origins. There is need to make the use of scales more precise.

Krogius (1958) discussed the variation in Kamchatkan sockeye salmon scales in considerable detail. She described the patterns found in the Kamchatka, Bolshaya, Ozernaya, Kukhtua, Pylga, and Paratunka Rivers, which include the major sources of sockeye salmon in Asia. Distinctive differences were found in the number of circuli formed in each year of fresh-water life, the size of the scale at the end of each year, and the relative numbers of crooked or broken circuli. Using these features, she identified Kamchatka, Ozernaya and Bolshaya River sockeye salmon taken in the North Pacific Ocean from Kamchatka to about long. 175° E. She stated that the origins of fish taken in the ocean could be determined from scales characteristics but that the method is in need of further development.

Kubo [21] reported the results of an extensive study of sockeye salmon scales and developed a method which he employed to identify the origin of maturing 5_2 and 6_3 salmon caught on the high seas. The first number in this terminology refers to the year of life when the fish was caught, and the subscript number to the year of life in which it migrated from fresh water. His scale comparisons included: (1) total radius (anterior), (2) length of anterior field for ocean growth only, the ratio of (2)/(1), the ratio of the spacing of ocean circuli 21 to 30 to ocean circuli 11 to 20 and the anterior radius of the fresh-water zone excluding the so-called "plus growth." Plus growth is indicated by the widely spaced circuli which in some fish follow the last fresh-water annulus and are believed to occur in fresh water just prior to the salmon's migration to the sea. He determined that the radius of the fresh-water growth zone was most efficient in identifying the origin of sockeye salmon in the high seas. Like Fukuhara et al. (1962), he concluded that the maturing sockeye salmon in the North Pacific Ocean and Bering Sea between Asia and long. 165° W. were principally of Kamchatkan or Bristol Bay origin in late May and June. He constructed and used frequency curves of fresh-water radii to correct for overlap in this character between Kamchatka and Western Alaska sockeye salmon. Figure 12 shows the adjusted result of identifying samples of salmon taken on the high seas.

The method employed by Kubo promises to be useful in determining the origin of salmon. His test for scale differences between sexes and the effect of fish length on scale characters might be improved by utilizing fish of a single, known origin instead of a high seas sample of unknown, and perhaps mixed, origin. A mixture of fish with varying scale characters might obscure the relationships he is examining. It is doubtful that any large error has been introduced, however.

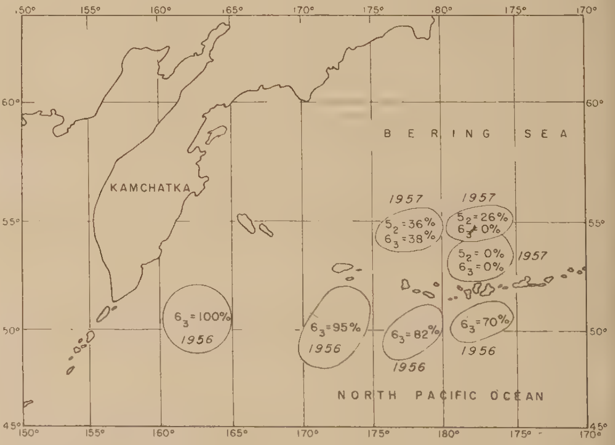

Figure 12.—Distribution of Asiatic sockeye salmon estimated by RF (fresh-water radius) composition in samples from various areas of the high seas.

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[21] Kubo, Tatsuro, Study of Sockeye Salmon Stocks by means of the Growth Pattern of Scales (Preliminary Report). Faculty of Fisheries, Hokkaido University, Japan (INPFC Doc. 206). August 1958, Part 1, 15 pp. (Text.) Part II–2, 16 pp.

The most serious difficulty with Kubo's results arises from the use of only the 5_2 and 6_3 fish. The failure to include the 4_2 and 5_3 groups prevents interpreting the results in terms of the relative numbers of Kamchatkan and Bristol Bay sockeye that may be present in the area. The proportion of the runs that return as 4_2, 5_3, 5_2, or 6_3 to Kamchatka or Bristol Bay varies widely from year to year. If only part of the fish are considered for any one year it is easily possible to overlook the major part of the maturing fish present. To illustrate this, table 5 shows the estimated numbers of fish of 4_2, 5_3, 5_2, and 6_3 categories that returned to Bristol Bay streams from 1956 to 1959. These figures are based on combined catch and escapement statistics. In 1956, 20.5 million of the 24.5 million fish returning to Bristol Bay were 4_2 and 5_3. Only 16 percent of the run was composed of 5_2 and 6_3 fish. In 1957 the situation was reversed. About 8.5 million returned as 5_2 and 6_3 fish, and they formed about 76 percent of the run of 11.1 million sockeye salmon. Therefore in a study in which only 5_2 and 6_3 fish were used, if the ocean distribution were the same for all age categories, estimates of the percent of the fish present of Bristol Bay origin would be expected to be very low in 1956 and high in 1957. Comparable figures are unfortunately not available for all major Kamchatkan streams.

TABLE 5.—*Age composition of Bristol Bay sockeye salmon runs*

[Figures in millions of fish]*

Year and District	4_2	5_3	Subtotal 2-ocean	5_2	6_3	Subtotal 3-ocean	Totals
1956							
Nushagak	0.914	0.316	1.230	1.090	0.126	1.216	2.446
Naknek-Kvichak	10.371	6.701	17.072	1.045	1.003	2.048	19.120
Ugashik	.528	.129	.657	.049	.057	.106	.763
Egegik	.292	1.326	1.618	.201	.418	.619	2.237
Totals	12.105	8.472	20.577	2.385	1.604	3.989	24.566
Percent	49.3	34.5	83.8	9.7	6.5	16.2	--------
1957							
Nushagak	.267	.033	.300	.659	.069	.728	1.028
Naknek-Kvichak	.018	1.953	1.971	5.187	1.217	6.404	8.375
Ugashik	.130	.117	.247	.261	.062	.323	.570
Egegik	.015	.158	.173	.260	.738	.998	1.171
Totals	.430	2.261	2.691	6.367	2.086	8.453	11.144
Percent	3.9	20.3	24.2	57.1	18.7	75.8	--------
1958							
Nushagak	1.139	.137	1.276	.946	.084	1.030	2.306
Naknek-Kvichak	.181	.561	.742	.080	.908	.988	1.730
Ugashik [1]	.024	.381	.405	.234	.085	.319	.724
Egegik	.002	.406	.408	.050	.257	.307	.715
Totals	1.346	1.485	2.831	1.310	1.334	2.644	5.475
Percent	24.6	27.1	51.7	23.9	24.4	48.3	--------
1959							
Nushagak	2.888	1.320	4.208	.436	.097	.533	4.741
Naknek-Kvichak [1]	1.307	2.684	3.991	1.030	.342	1.372	5.363
Ugashik [2]	--------	--------	--------	--------	--------	--------	--------
Egegik [2]	--------	--------	--------	--------	--------	--------	--------
Totals	4.195	4.004	8.199	1.466	.439	1.905	[3] 10.104
Percent	41.5	39.6	81.1	14.5	4.3	18.9	--------

[1] Age composition estimated from catch samples only.

[2] Not available.

[3] Total run to the four districts was 12.622 million fish in 1959. Thus, the percentages given fairly accurately depict age composition of total Bristol Bay run in 1959.

*From research files of the University of Washington Fisheries Research Institute and the Bureau of Commercial Fisheries.

When figure 12 is considered with the data of table 5, it appears that the estimates of the numbers of Asian fish given for the North Pacific Ocean are probably high, because only 1956 samples are considered. Bristol Bay fish would be under-represented. The run to Bristol Bay was relatively large in 1956, but the dominant age categories involved did not enter the calculations. Kamchatkan runs appear to have high percentages of 5_2 and 6_3 fish every year. The degree to which bias occurs is determined by the relative proportions of fish of the same age categories in the runs to Kamchatka and Bristol Bay, and by whether fish from both origins are present at the time and place of sampling.

Kubo and Kosaka [22] reported a similar study which was concerned only with the origin of 5_3 sockeye salmon caught on the high seas. Because the anterior radii of the fresh-water zones (from the focus to the last fresh-water annulus) was distinctly larger in fish which matured as 5_3 than those which remained in the ocean and matured as 6_3, they concluded that the radius of the fresh-water zone was not suitable to separate Kamchatkan and Bristol Bay sockeye salmon. The maturity of the samples was not considered to be known with sufficient certainty. Therefore a 5_3 taken at sea might actually have remained to migrate as a 6_3 a year later.

They further concluded that the anterior radius of the fresh-water zone divided by the combined width of the first two ocean zones provided the best means of identifying the origin of maturing 5_3 sockeye salmon in the Aleutian Islands area. Although it is not explicitly stated, the 1956 samples from the Kamchatka region and from

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[22] Kubo, Tatsuro, and Jun Kosaka, Study of Sockeye Salmon Stocks by means of the Growth Pattern of Scales, Fisheries Agency, Japan (INPFC Doc. 326), August 1959, 8 p.

Bristol Bay were evidently employed to define the population parameters that were used to calculate the percentage of high seas fish of Kamchatkan and Bristol Bay origins. The results of these calculations are shown in figure 13.

These results are difficult to interpret for the reasons discussed in connection with Kubo's 1958 report.

Neither of the above papers provides a method of judging the accuracy with which high seas samples are assigned to the correct origin. An empirical test in which independent samples of known origin are identified would be useful. It would still be necessary, however, either to find some means of weighting the samples or to develop a method by which all of the age categories caught could be suitably treated. Without this, there is no way of knowing what portion of the fish in any particular sample originated in Kamchatka or Bristol Bay.

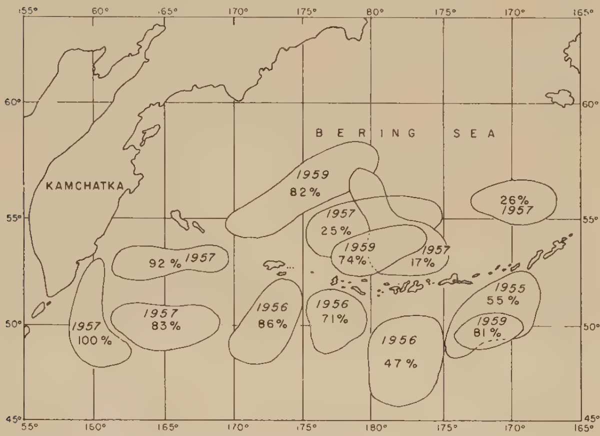

FIGURE 13.—Distribution of Asiatic 5_3 age group sockeye salmon estimated by RF/RS_2 ratio (fresh-water radius/radius to fourth annulus) composition in samples from various areas of the high seas (from Kubo and Kosaka, 1959).

Mosher[23] in a similar study examined the number of circuli in the fresh-water zone and first ocean zone of sockeye scales. Scale samples taken in or near Kamchatka and in Bristol Bay streams provided the population parameters and a test of the accuracy of his identifications.

The fish were divided according to whether they had migrated to sea in their second, third, or fourth years and whether the sample came from Kamchatka or Bristol Bay streams. For each of the six categories a bivariate tabulation was made of the number of circuli in the fresh-water and first ocean year zones, except for the fourth year fish for which length of these zones was used. The bivariate frequencies were then weighted to 100 to adjust for unequal sample size. Next, the frequencies were superimposed, the Kamchatkan frequencies being placed on those for Bristol Bay of the same fresh-water age. The numbers in each cell were compared, and each cell was judged to be Kamchatkan or Bristol Bay according to which had the larger frequency.

When the 1957 samples of maturing fish of known origin which were used to construct the tables were identified by using the bivariate charts, 85.4 percent of the fish from near Kamchatka and 86.5 percent of the fish from Bristol Bay were correctly identified. Of an additional 261 scale samples from near or in Kamchatka in 1957, which were not used in deriving the continental standards (for lack of data on the area of the fish from which scales were taken), 237 or 91 percent were correctly assigned to Kamchatka.

Samples of fish taken in other years were also used to examine the accuracy of the classificatory procedure. Of 648 sockeye salmon taken in or near Kamchatka and 786 sockeye taken from Bristol Bay in 1956, 77.2 percent and 82.3 percent respectively were correctly identified.

For 1955 samples (again using the 1957 reference data) 77 percent of 168 Asian fish and 72 percent of 303 Bristol Bay fish were correctly identified. The average misclassification was roughly 14 percent for the 1957 samples, 21 percent for the 1956 samples, and 25 percent for the 1955 samples. This seems to indicate a moderately increasing error in classification as the year in which the standards were taken becomes more remote. No difference was found between sexes in the scale characters.

Using the charts developed with 1957 inshore samples, Mosher classified the sockeye salmon in high seas samples for 1956 and 1957. The initial classifications of the fish into area of origin were adjusted for the average error of misclassification for that year (fig. 14). The average

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[23] Mosher, Kenneth H., Racial analysis of the offshore samples of red salmon (*Onchorhynchus nerka*, Walbaum) from central north Pacific and Bering Sea from May 1 to July 15, 1956–57 by means of scales. Bureau of Commercial Fisheries, Seattle, Wash. (INPFC Doc. 312), October 1959, 29 p. [Processed.]

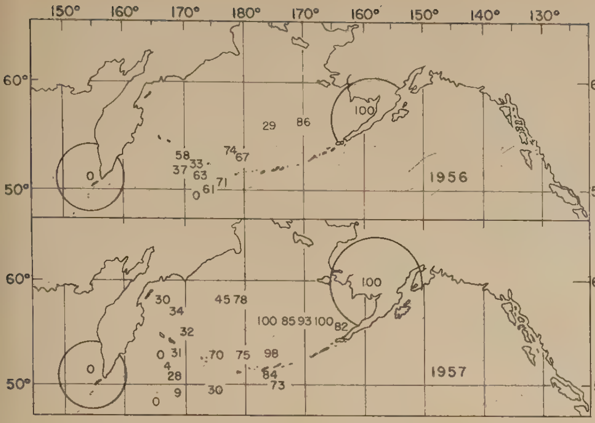

FIGURE 14.—Percentage of Bristol Bay type sockeye salmon in scale samples taken from mid-May to mid-July.

adjustment of 21 percent produces a bias favoring Bristol Bay fish in 1956.

There are other possible sources of bias. The high seas samples used were mostly maturing fish, but contained some immature fish, especially in July. The samples contained a mixture of fish of various year classes and age categories. No definitive mention is made of the variation that might occur in the scale characters of the high seas samples due to differing year classes, ages of maturity, length selectivity, or similar factors. Kubo and Kosaka[24] presented data which indicated that the anterior radius of the fresh-water zone was larger among those fish which matured in 1956 as 5_3 than in fish of the same brood year which returned in 1957 as 6_3. The effect of this on Mosher's results is obscure. Further, the error of misclassification is given for the combined samples; it is not clear whether or not this error was the same for all three fresh-water ages. If it were markedly different, the adjustments could be inaccurate.

With only moderate increases in error, Mosher, however, was able to identify the continental origin of sockeye in samples from years (1955 and 1956) other than that used in constructing the tables. This would indicate that differences between adjacent year classes or variations in life history do not upset the method. Consequently, the inclusion of immature fish on the high seas should not introduce serious error.

Mosher, Anas, and Liscom (1961) applied the same method to the 1958 high seas samples. Using 1958 samples taken near Kamchatka, they determined an average error of misclassification of 28.8 percent for 584 Asian fish; using Bristol Bay samples yielded a 15.6 percent error for Bristol Bay fish. These errors were applied as adjustment factors to estimate the numbers of Kamchatkan and Bristol Bay sockeye in the high seas samples (fig. 15).

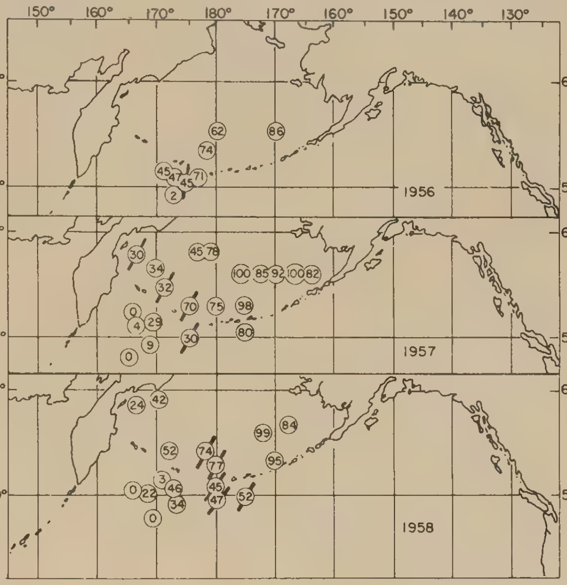

FIGURE 15.—Percentage of Western Alaska type sockeye salmon in scale samples taken from mid-May to mid-July (from Mosher et al., 1961). Samples containing more than 25 percent immature fish have been marked with a diagonal line.

Excepting the bias factor, this paper shares the difficulties discussed for Mosher,[25] as well as the benefit of general verification by empirical means. A further problem appears when the results of classification of the 1956 samples are compared (figs. 14 and 15). In figure 15 the 29 percent sample at about long. 175° W. in figure 14 is no longer present, and the seven samples shown for the western North Pacific Ocean in 1956 in figure 14 became five samples in figure 15. Mosher has stated (personal communication) that these changes have been brought about by correction of errors, revision of the manner in which the samples were grouped, elimination of very small samples, and elimination of immature fish. In some instances the original groups contained samples from quite different times and places.

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[24] See footnote 22, p. 465.

[25] See footnote 23, p. 466.

Because the distributions of maturing and immature sockeye salmon are different, further separation in the samples used by Mosher, Anas, and Liscom is desirable. The original data have been examined, and those samples shown in figure 15 that contained more than 25 percent immature fish are marked by a diagonal line. If these samples are omitted when considering the origins of the salmon, the major change is an absence of midocean samples. Those which remain are similar to the adjacent ones deleted.

As stated in the proceedings of the Seventh Annual Meeting of the International North Pacific Fisheries Commission,[26] the Asian standards are not necessarily adequate for estimating the proportion of Asian stocks in samples from near northeast Kamchatka. Nevertheless, the studies indicate for 1956, 1957, and 1958 that in the period from mid-May until mid-July in the Bering Sea, maturing sockeye salmon of Kamchatkan origin predominated from Kamchatka to long. 170° E. and occurred at least to long. 180°. In the North Pacific Ocean they were generally predominant to about long. 175° E. Bristol Bay fish were predominant from Bristol Bay to west of long. 180° in the Bering Sea.

Using scales,[27] Mosher, Anas, and Liscom (1961) tentatively identified high seas caught sockeye salmon to be from the British Columbia coast. These studies suggested that maturing fish of the River's Inlet and Smith Inlet types were found in the Gulf of Alaska as far west as long. 155° W. and that immature fish from these areas were found as far west as long. 170° W.

PARASITE STUDIES

Margolis (1963) reported the use of parasites to detect the continent of origin of sockeye salmon taken on the high seas. He found that a larval tapeworm, *Triaenophorus crassus*, was acquired by sockeye salmon in their early life in fresh water. It was found in smolts and returning spawners only in certain areas of western Alaska, chiefly in Bristol Bay, but not in Asian sockeye salmon. A nematode, *Dacnitis truttae*, was found in samples of sockeye salmon taken near Kamchatka and in the Okhotsk Sea, but was not found in any samples of smolts or adults from North American rivers. This parasite also infects the young fish while in fresh water. Thus, he identified two "tags," one limited to western Alaskan and the other to Kamchatkan sockeye salmon. While the incidence of the parasites varies between years and streams, *Triaenophorus* seems to be more prevalent in Bristol Bay sockeye than is *Dacnitis* in Kamchatkan fish. His report shows levels of 4 to 12 percent of Kamchatkan samples infected with *Dacnitis* and 3.5 to 21.7 percent of the Bristol Bay samples infected with *Triaenophorus*.

Margolis' work reports are valuable in determining the origin of salmon stocks found on the high seas. The presence of *Dacnitis* or *Triaenophorus* in a sample is positive evidence of the origin of the fish bearing the parasites. The origin of the uninfected fish in samples is harder to interpret. Because of the variable and often low level of infection, some samples of Kamchatkan or Bristol Bay sockeye probably would not contain any infected fish. It is also possible that some samples containing no infected fish were sockeye which originated in neither Kamchatka nor Bristol Bay. Therefore it is difficult to place any quantitative interpretation on the fact that *Dacnitis* has never been found in maturing sockeye salmon east of long. 175° E. in the North Pacific Ocean or that *Triaenophorus* has never been found in maturing sockeye salmon west of long. 168° E. It would seem, however, that they do not ordinarily exceed these limits in large numbers during the May–June sampling period.

More samples were taken for parasite studies in 1959 than in any other year. Data from these samples indicated that between 10 and 13 percent of the sockeye salmon returning to Bristol Bay were infected by *Triaenophorus*. When this range of infection is compared with the rates of infection in the high seas samples (fig. 16, from Margolis, 1963) it is possible to reach some conclusions concerning the origin of maturing sockeye salmon occurring in oceanic areas in May and June of 1959. It is evident that, in many of the high seas samples, the incidence of *Triaenophorus* closely resembled the rate of infestation found in Bristol Bay sockeye

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[26] See footnote 3.

[27] Manzer, J. I., T. H. Bilton, and K. H. Mosher, The ocean distribution of sockeye salmon originating in rivers and Smith Inlet, Fisheries Research Board of Canada and Bureau of Commercial Fisheries (INPFC Doc. 407), October 1959, 5 pp. [Processed.]

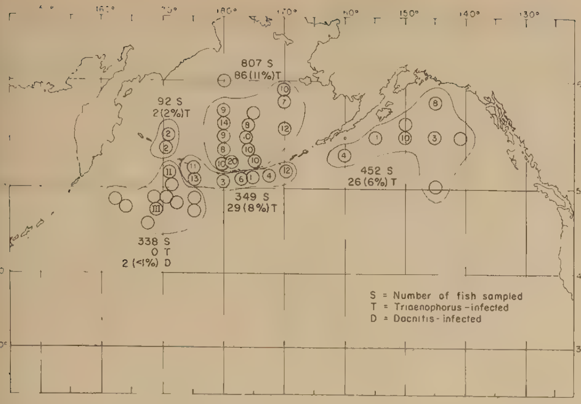

FIGURE 16.—Percentage of infected sockeye salmon in samples of maturing fish in 1959 (Margolis, 1963).

salmon. On this basis it is probable that these samples are comprised mainly of Bristol Bay sockeye salmon. This probability requires that Bristol Bay salmon of each river and each age group have the same relative distribution at sea. July and August are not shown, because as stated earlier, maturing fish become relatively scarce then.

The following summary [28] succinctly outlines the conclusions which may be drawn from this study:

(1) In the Bering Sea from 170° W. to 180° samples taken in the latter half of June consisted largely of fish of Bristol Bay origin. Between 180° and 171° E. samples were lacking. At 171° E. in early June the proportion of Bristol Bay sockeye in the two samples examined was greatly reduced. Presumably the majority of sockeye in these samples were of Asian origin. Samples of maturing fish from west of 171° E. in the Bering Sea were not obtained.

(2) Immediately south of the Aleutians, from about 169° W. to 175° E. in late May and early June, there was greater variation in the incidence of *Triaenophorus* between samples than in the eastern half of the Bering Sea and no trend was evident. The combined samples in this area consisted predominantly of fish of Bristol Bay origin, but to a lesser extent than in the eastern half of the Bering Sea. The area of origin of the maturing sockeye other than those from Bristol Bay could not be determined. Samples from close to the south side of the Aleutians west of 175° E. were not examined.

(3) To the south and west of the waters bordering the extreme western Aleutians, from 175° E. and westward, no Bristol Bay sockeye, but two Asian sockeye, were identified in the samples collected from late May to late June. It seems most likely that the maturing sockeye in these samples were mainly of Asian origin.

In the Gulf of Alaska in a sample of maturing sockeye taken towards the middle of June at 55° N., 155° W., and in samples taken in late May at 55° N., 150° W., and 58° N., 145° W., a large proportion were of Bristol Bay origin. Toward mid-June Bristol Bay sockeye appeared to be absent from a sample taken at about 55° N., 155° W., suggesting that maturing Bristol Bay sockeye move out of the Gulf of Alaska quite rapidly. Eastward from 150° W., along 55° N., in the latter half of May the proportion of Bristol Bay sockeye diminished and none were identified at 141° W. It seems most probable that the predominant stocks of sockeye in these samples from the eastern Gulf of Alaska were from North American areas to the south and east of the Alaska Peninsula.

Although most Bristol Bay maturing sockeye were found in samples taken in late May or June, two were also identified in Bering Sea samples (at 170° W. and 173° E.) taken in early July and one in the mid-Aleutian area in early August.

The results obtained from the 1959 samples of maturing sockeye confirm and considerably extend the results obtained from examination of less adequate samples of the years prior to 1959, as presented in Document 303.

The parasite studies also add much to our knowledge of the origin of the immature fish caught at sea. Immature sockeye salmon from Kamchatka were found from Kamchatka to as far east as long. 170° W. in the North Pacific Ocean and as far east as long. 175° W. in the Bering Sea. Immature salmon from Bristol Bay were found as far east as long. 145° W. and as far west as long. 175° E. in the North Pacific Ocean. In the Bering Sea, immature Bristol Bay sockeye salmon were found as farwest as long. 170° E. One was taken in 1958 about 30 miles southeast of Cape Olyutorski in Asia.

SEROLOGICAL STUDIES

Investigations have been undertaken to discover blood differences that could be used to identify the streams of origin of sockeye salmon caught on the high seas. Ridgway and Klontz (1960) demonstrated the existence of blood groups in salmon and through isoimmunization showed that considerable antigenic diversity exists in sockeye salmon. Ridgway, Cushing, and Durall (1958) found differences in the reactions of sockeye salmon erythrocytes with pig sera. The degree of reaction was found to differ between sockeye salmon from different streams. There was considerable evidence that the differences in reactions were genetically controlled.

Ridgway, Klontz, and Matsumoto (1962) reported the development of a modification of Ouchterlony's method of double diffusion precipitin analysis in agar and its application to the problem of identifying the origin of sockeyes almon taken on the high seas. They found that antiserum produced by injecting rabbits with sockeye salmon serum reacted with the serum of 96.8 percent of the sockeye salmon taken from American streams, and only 7.9 percent of the samples taken near Kamchatka. By testing sera from hatchery-reared fish, they were able to show that the antigens responsible for the reaction were present for at least a year prior to maturation, and that the antigens are a sufficiently permanent feature of the salmons' sera for use in identifying the origin of fish taken at sea.

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[28] See footnote 3, p. 450.

The serological method was difficult to apply to high seas samples. It became apparent that the method of handling and storing the samples from the high seas was either partially destroying the antigens in the blood of American fish or inhibiting the reaction. The portions of the samples taken in the eastern Bering Sea in June identified as North American by Ridgway, Klontz, and Matsumoto seem to be lower than might be reasonably expected. This is not clearly evident in their tables, because the samples are small and no distinction is made between mature and immature salmon. Because the distribution of immature sockeye salmon is not the same as that for maturing individuals, it is not possible to make direct quantitative comparisons between this work and the studies using tagging, morphology, scales, and parasites.

The Japan Fishery Agency [29] reported the results of experiments with the haemoglobin fraction of the blood of sockeye salmon. It was possible to identify three separate groups of samples from the Pacific Ocean and Bering Sea. The samples taken south of the central Aleutian Islands were more similar to those taken near Kamchatka than were the samples taken north of the Aleutian Islands.

DISCUSSION

We have considered briefly the several techniques employed to determine the origin of the maturing sockeye salmon found in the high seas. Our information is more complete for the fish in the sea between long. 165° W. and Kamchatka than for fish in waters to the east. In the Pacific Ocean west of long. 165° W., it appears that the salmon mainly move north and west in the spring; those going to Kamchatka continue west, and those going to Bristol Bay pass into the Bering Sea and turn east. There is an area between long. 180° and 170° E. (and possibly wider) that for a time may contain large numbers of fish from both of these sources. As these fish continue their homeward migration, segregation into stream groups becomes increasingly complete. The relative numbers of maturing fish from Kamchatka and Bristol Bay that may be found in the area of mixing in May and June probably varies with the year and date of sampling.

The runs of fish to the rivers vary widely in size from year to year (table 3). If, for example, the spatial distribution at sea of Kamchatka River fish were identical from year to year, they would certainly be scarcer at sea at a particular place and time in years when the stock for that river was low. We would then expect the percentage of fish from a particular area to fluctuate in accord with their abundance, unless all of the stocks found in that part of the sea were undergoing similar fluctuations. Because there seems to be no close year-to-year relationship in these fluctuations between Kamchatka and Bristol Bay, we may expect that the percentage of the fish from both of these will fluctuate in the high seas samples taken in the area of mixing.

In the period 1956–59, both Kamchatka and Bristol Bay appear to have had salmon runs of widely varying numbers. The 1956 Bristol Bay run of 24.6 million fish was fairly large, and the 1958 run of 5.5 million fish was fairly small. The sizes of the Kamchatka runs are not as well known, but the 1957 run might have been quite large. Unless the bulk of the Japanese high seas catch of 20.1 million fish were of Bristol Bay origin, the potential run to Kamchatka in 1957 must have been numerous, at least at sea. The high seas catch might not have been preponderantly from Kamchatkan sockeye salmon, however, It is not clear whether maturing sockeye salmon from a particular stream are distributed in the same relative manner from year to year. The available data do not seem to allow more than speculation on this point. From table 5, however, it is evident that the age composition of the stocks returning to an area may vary between years. In 1956 the Bristol Bay runs were mainly fish which had spent 2 years at sea; in 1957 the runs had predominantly spent 3 years at sea. Unless the immature fish return to the same part of the ocean to spend each succeeding winter, it is conceivable that those fish which remain at sea an additional year might become more dispersed.

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[29] Japan Fisheries Agency, Studies to determine the origin of northern sea salmon by serological methods, Fisheries Agency, Japan (INPFC Doc. 222), October 1958, 21 p. [Processed].

EFFECT OF TIME OF SAMPLING

In addition to the sources of variation mentioned above, it is pertinent to examine the distribution of the samples in time. Because the maturing fish are moving rapidly to their home streams, samples, unless taken sufficiently early in certain areas, could not be expected to contain fish from the more distant streams. Jones (1961) provided data on the rate of travel of sockeye salmon from various points on the high seas to Bristol Bay, Alaska. Some variation was evident in the mean rate of travel for fish tagged at different locations, and he stated that the salmon tagged later traveled more rapidly. Assuming that the tagged fish traveled in a straight line from Adak Island to their final destination, he found that the average rate of travel per day varied from about 22 to 34 nautical miles. A mean rate of 30 nautical miles per day for Bristol Bay sockeye salmon seems reasonable. This rate, which would place the peak of the Bristol Bay runs between long. 180° and long. 175° W. in mid-June and near the Pribilof Islands in late June, which is in agreement with fishing information. It is not clear whether the rates presented by Taguchi and Nishikawa or Sato are suitable for this use because they deal with inshore movements.

Jones's study provides a basis for examining the effect of date of sampling upon the number of Bristol Bay salmon found in a sample. A mean migration rate of 30 miles per day was used to construct figure 17. The time of migration was calculated from lat. 50° at various meridians along straight lines to Bristol Bay streams. The end of the period of peak run in Bristol Bay was considered to be July 15. The dates at which most of these fish would have passed these meridians were estimated, and the diagonal line for Bristol Bay located on the figure. We would then expect that samples occurring above this diagonal would have been taken too late to contain Bristol Bay fish at that particular longitude. Because variation in latitude of sampling introduces distance discrepancies, only samples taken in the Pacific Ocean were used. This does not eliminate all of the variation, and the position of the diagonal line is not precise with respect to the samples shown. The samples listed in Fukuhara et al. (1962), Fukuhara (1961), and Landrum and Dark (1963), were used to examine the effect of sampling time upon the classification of the fish in the samples.

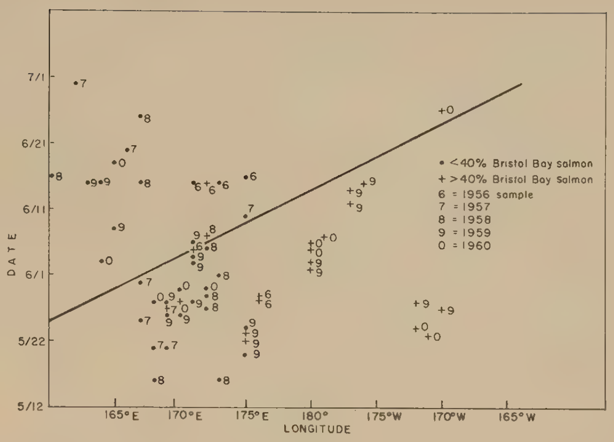


Figure 17.—Effect of time of sampling on origin of samples from Pacific Ocean. Samples below line could contain fish from Bristol Bay if we accept a 30-mile per day homeward migration. Lines are based on distances from stream to lat. 50° N. for various longitudes. Samples from Fukuhara et al., 1962; Fukuhara, 1961; and Landrum and Dark, 1963.

The 1956 samples were all taken in the vicinity of long. 170° E. to 175° E., and one sample estimated to contain more than 40 percent Bristol Bay fish was taken 9 days later than might have been expected. The runs in Bristol Bay, however, were still quite heavy after July 20, 1956, which might account for apparent discrepancy.

When the data for the 5 years together are examined the migration rate of 30 miles per day is reasonably consistent with the results of morphological classification. Excepting the sample in 1956, all of the samples taken in the North Pacific Ocean that were found to contain more than 40 percent Bristol Bay sockeye salmon fall either very near to the Bristol Bay "disappearance line" or below it, as predicted. The line seems reliable in 21 of 22 instances. If we accept this, we must then suspect that over one-third of the sampling was too late to detect the distribution of maturing Bristol Bay salmon west of long. 180° in the North Pacific Ocean. This would tend to depress the average percentages of maturing Bristol Bay fish found in the western samples for the May–June period.

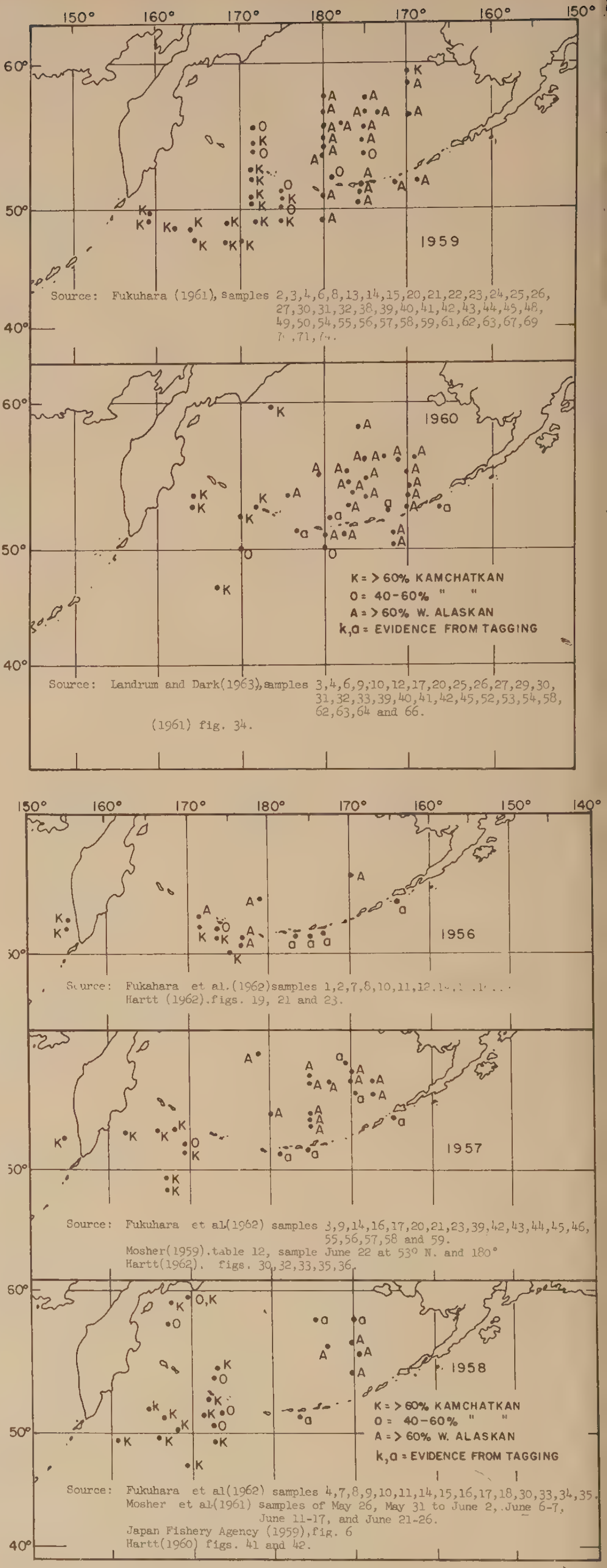
Because of the uncertainty of the migration rates for Kamchatkan sockeye salmon, figures for these runs are not presented. However, if July 5 and August 5 are used as the end of the period of peak runs for the Kamchatka River and the Ozernaya River, respectively, and a 30-mile per day migration rate is assumed, it is found that sampling in the North Pacific Ocean west of long. 180° and lat. 50° N. has been done early enough to intercept these runs. There seems, however, to be very little information available to establish the rate of travel for these fish, although it should be possible to make estimates from the detailed records of the Japanese high seas fisheries.

ORIGIN OF SOCKEYE SALMON

It is worthwhile to consider together the results of morphology, scale, and tagging studies to see what quantitative conclusions may be drawn concerning the origin of maturing red salmon on the high seas. Although the distribution of sampling is neither regular nor complete for any technique during 1956–60, some estimates can be obtained because one study sometimes provides information where another does not.

The combined results of the studies during 1956–60 for maturing fish in late May and June are shown in figure 18. The results of the morphology and scale studies are taken directly from the sources cited earlier. Tagging results were employed only where the migration from the point of tagging appeared to be wholly to Asia or North America. Where more than one method gave the same result for a locality, only one was plotted. In the instance where two methods gave divergent results, both were entered. For this figure, samples which yielded estimates of more than 60 percent Kamchatkan salmon were considered dominantly Kamchatkan (K); those with estimates of 40 to 60 percent were considered indeterminate (O), and those with estimates of over 60 percent Western Alaska type were considered to be Western Alaska sockeye salmon (A).

These figures show: (1) No examples of dominance of maturing Kamchatkan salmon east of long. 175° E. in May and June 1956, 1957, 1958, 1959, and 1960 with the exception of one sample in the eastern Bering Sea in 1959 which is considered to have been too far from Kamchatka on June 27 to be reasonably considered as Kamchatkan. (2) Data for the Western Bering Sea are scanty. The few observations available suggest that the dividing line between areas



Source: Fukuhara (1961), samples 2,3,4,6,8,13,14,15,20,21,22,23,24,25,26, 27,30,31,32,38,39,40,41,42,43,44,45,48, 49,50,54,55,56,57,58,59,61,62,63,67,69 [illegible],71,[illegible].

Source: Landrum and Dark(1963), samples 3,4,6,9,10,12,17,20,25,26,27,29,30, 31,32,33,39,40,41,42,45,52,53,54,58, 62,63,64 and 66.
(1961) fig. 34.

Source: Fukahara et al.(1962)samples 1,2,7,8,10,11,12,[illegible]
Hartt (1962).figs. 19, 21 and 23.

Source: Fukuhara et al(1962) samples 3,9,14,16,17,20,21,23,39,42,43,44,45,46, 55,56,57,58 and 59.
Mosher(1959).table 12, sample June 22 at 53° N. and 180°
Hartt(1962). figs. 30,32,33,35,36.

Source: Fukuhara et al(1962) samples 4,7,8,9,10,11,14,15,16,17,18,30,33,34,35.
Mosher et al(1961) samples of May 26, May 31 to June 2, June 6-7, June 11-17, and June 21-26.
Japan Fishery Agency (1959),fig. 6
Hartt(1960) figs. 41 and 42.

FIGURE 18.—Origin of maturing sockeye salmon in May and June.

dominated by Kamchatkan and Western Alaska sockeye salmon was about long. 175° E. (3) Maturing Western Alaska salmon were dominant in the Bering Sea to or west of long. 180° in the 4 years (1956, 1957, 1959, and 1960) for which samples were available. There was only one sample near long. 180° in 1956 and none in 1958. (4) Dominance of Bristol Bay fish in the North Pacific Ocean west to long. 175° E. in 1956, to long. 177° W. in 1957 (with no data between long. 177° W. and 170° E.) to long. 180° in 1959, and west of long. 180° in 1960.

According to the studies that have been discussed in the previous paragraphs, and the results of parasitological studies (fig. 16), there appears to be a zone of about 10 degrees of longitude (from long. 170° E. to long. 180°) between the areas consistently dominated by maturing Kamchatkan or Bristol Bay sockeye salmon in May and June.

With the data in figure 18, it is possible to summarize the results of the studies of the origin of maturing sockeye salmon as follows: For the 5 years 1956, 1957, 1958, 1959, and 1960, the samples in the Bering Sea near and east of long. 180° are generally heavily dominated by Bristol Bay salmon. Bristol Bay salmon dominated one sample near long. 180° in 1956, two in 1957, seven in 1959, including one at long. 175° E., and three in 1960. Near long. 175° W., however, there are six samples in 1957, two in 1958, five in 1959, and eight in 1960 that show an eastward continuation of Bristol Bay dominance observed at long. 180° in the Bering Sea. Because these years include both very large and very small runs in Bristol Bay and considerable variation in the hydrography of the area, it appears that maturing Bristol Bay sockeye consistently dominate the sockeye salmon catches in the Bering Sea near and east of long. 180°.

The situation in the North Pacific Ocean appears to be somewhat different (fig. 18). The data for 1956, 1958, and 1959 indicate a dominance of Kamchatkan sockeye salmon as far east as long. 175° E., with little information on the eastward extent of Kamchatkan dominance in 1957 and 1960. Dominance of Bristol Bay salmon is indicated as far west as long. 175° E. in 1956 and 1960, and as far west as long. 180° in 1957 and 1959. Data for the central Aleutian Islands area are almost lacking in 1957 and 1958. Figure 17 shows that west of long. 180° four of the 1956 samples, three of the 1957 samples, three of the 1958 samples, three of the 1959 samples, and two of the 1960 samples were taken too late to have intercepted the Bristol Bay runs. In those samples taken sufficiently early, we find strong representation of Bristol Bay fish to long. 175° E., with lesser numbers appearing to the westward. The samples taken west of long. 175° E. prior to the time that Bristol Bay fish might have left mainly show dominance of Kamchatkan salmon in each year. It can be tentatively concluded, therefore, that dominance shown for Kamchatkan fish west of long. 175° E. is not primarily caused by time of sampling, and that the data support the view that the maturing sockeye salmon were predominantly of Kamchatkan origin.

The samples of maturing sockeye salmon taken in May and June in the North Pacific Ocean east of long. 180° (fig. 18) were preponderantly of Bristol Bay origin from 1956 to 1960. No indication of dominance by Kamchatkan salmon is found in the results of either the morphological or tagging studies.

It appears from these data that maturing Bristol Bay sockeye dominate the North Central Pacific Ocean as far west as long. 180° in late May and in June. The change in sockeye samples from predominantly fish of Alaska origin to predominantly fish of Kamchatka origin appears to occur near long. 175° E. In the Bering Sea in late May and in June maturing Bristol Bay fish are consistently dominant westward to at least long. 180°. We may conclude that the dominance of Kamchatkan and Bristol Bay sockeye salmon in these areas are consistent features of the system of distribution under the conditions prevailing during the 5 years of observation.

CONCLUSIONS

1. On the basis of catch statistics, Asian stocks of sockeye salmon provide about 23 percent of the total catch and North American stocks about 77 percent.

2. Sockeye salmon enter their home streams from May until October, but for any stream the duration of heavy migration is usually less than 1 month.

3. Sockeye salmon are found from North America to Asia in the North Pacific Ocean during spring and summer. Information is lacking for fall and winter.

4. The oceanic distribution appears to shift southward in winter and northward in summer.

5. Immature Asian sockeye salmon have been shown to migrate as far east as long. 170° W. in the North Pacific Ocean and long. 175° W. in the Bering Sea. Immature Bristol Bay sockeye have been shown to migrate as far east as long. 145° W. and as far west as long. 173° E. in the North Pacific Ocean, and as far west as long. 170° E. in the Bering Sea.

6. In May and June maturing Kamchatkan sockeye salmon predominate in the North Pacific Ocean from Kamchatka to about long. 175° E. and Bristol Bay sockeye salmon predominate westward to at least long. 180°. Maturing Kamchatkan sockeye salmon have been tagged as far east as long. 165° E. and Bristol Bay fish have been tagged as far west as long .167° E. In the Bering Sea, maturing sockeye salmon are almost entirely of Bristol Bay origin from Bristol Bay to west of long. 180°.

7. The major areas dominated by Kamchatkan or Bristol Bay sockeye salmon appear to have been consistent in 1956, 1957, 1958, 1959, and 1960.

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LITERATURE CITED

ANDREW, F. J., AND G. H. GEEN.
1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. International Pacific Salmon Fisheries Commission, Bulletin XI, 259 pp.

BIRMAN, I. B.
1958. [On the occurrence and migration of Kamchatka salmon in the northwestern part of the Pacific Ocean.] O rasprostranenii i migratsii͡akh kamchatskikh lososĕi v severo-zapadnŏi chasta Tikhogo okeana. *In* Materialy po biologii morskogo perioda zhizni dal'nevostochnykh lososĕi, pp. 31–51. Vsesi͡uznyi Nauchno-issledovatel'skii Institut Morskogo Rybnogo Khozi͡aĭstva i Okeanografii (VNIRO). [Translation by R. E. Forester, 24 pp., Fisheries Research Board of Canada, Translation Series No. 180.]

FOERSTER, R. E.
1955. The Pacific salmon (genus *Oncorhynchus*) of the Canadian Pacific Coast, with particular reference to their occurrence in or near fresh water. International North Pacific Fisheries Commission, Bulletin No. 1, pp. 1–56.

FOSKETT, D. R.
1953. Contributions to the life history of the sockeye salmon (No. 38). Province of British Columbia, Provincial Department of Fisheries Report for year ended December 31, 1952, pp. L33–L56.

FUKUHARA, F. M.
1961. Analysis of red salmon morphological data—1958 and 1959. International North Pacific Fisheries Commission, Annual Report, 1960, pp. 99–107.

FUKUHARA, F. M., S. MURAI, J. J. LALANNE, AND A. SRIBHIBHADH.
1962. Continental origin of red salmon as determined from morphological characters. International North Pacific Fisheries Commission, Bulletin No. 8, pp. 15–109.

GILBERT, CHARLES H.
1914–1920. Contributions to the life history of the sockeye salmon. (Nos. 1–6). Province of British Columbia, (Annual) Report of the Commission of Fisheries for the years 1913–19. Various pagination.

HANAVAN, M. G.
1961. Distribution and racial sampling of salmon on the high seas. International North Pacific Fisheries Commission, Annual Report for the year 1960, pp. 76–81.

HARTT, ALLAN C.
1962. Movement of salmon in the North Pacific Ocean and Bering Sea as determined by tagging, 1956–1958. International North Pacific Fisheries Commission, Bulletin No. 6, 157 pp.
1963. Tagging studies [in 1961]. International North Pacific Fisheries Commission, Annual Report, 1961, pp. 83–91.

HIRANO, YOSHIMI.
1953. The outline of results of tagging experiments on the Pacific salmon. Hokkaido-ritsu Suisan Shikenjo, goju Shunen Shuppan (Hokkaido Government Fisheries Research Station, 50th Anniversary Publication), 134 pp. [In Japanese, with English abstract pp. 44–46.]

INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION (INPFC).
1957. Annual report for the year 1956. International North Pacific Fisheries Commission. 88 pp.
1958. Annual report for the year 1957. International North Pacific Fisheries Commission, 86 pp.
1959. Annual report for the year 1958. International North Pacific Fisheries Commission. 119 pp.

1960. Annual report for the year 1959. International North Pacific Fisheries Commission. 116 pp.

1961. Annual report, 1960. International North Pacific Fisheries Commission, 116 pp.

1963. Annual report, 1961. International North Pacific Fisheries Commission. 127 pp.

INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION.

1959. Annual report, 1958. International Pacific Pacific Salmon Fisheries Commission, 33 pp.

1961. Annual report, 1960. International Pacific Salmon Fisheries Commission, 36 pp.

ISHIDA, TERUO, AND KIICHI MIYAGUCHI.

1958. On the maturity of Pacific salmon (*Oncorhynchus nerka, O. keta,* and *O. gorbuscha*) in offshore waters, with reference to the seasonal variation in gonad weight. Bulletin of the Hokkaido Regional Fisheries Research Laboratory (Yoichi, Japan) No. 18, pp. 11–22. [In Japanese, with English summary. Translation by Kunio Yonezawa, 7 pp., Fisheries Research Board of Canada, Translation Series No. 190.]

JAPAN FISHERIES AGENCY.

1959. Report of research on salmon conducted by Japan in 1958 for the International North Pacific Fisheries Commission. International North Pacific Fisheries Commission, annual report for the year 1958, pp. 50–73.

1960. Report on the investigations by Japan for the International North Pacific Fisheries Commission—1959. International North Pacific Fisheries Commission, Annual report for the year 1959, pp. 54–78.

1961. Report on the research by Japan for the International North Pacific Fisheries Commission during the year 1960. International North Pacific Fisheries Commission, Annual report for the year 1960, pp. 57–75.

1963. Report on research by Japan for the International North Pacific Fisheries Commission during the year 1961. International North Pacific Fisheries Commission, Annual report for the year 1961, pp. 48–82.

JONES, B. F.

1961. Ocean migration of Pacific salmon revealed by tagging and recovery. International North Pacific Fisheries Commission, Annual Report, 1960, pp. 108–115.

KILLICK, S. R., AND W. A. CLEMENS.

1963. The age, sex ratio and size of Fraser River sockeye salmon 1915 to 1960. International Pacific Salmon Fisheries Commission, Bulletin XIV, 140 pp.

KROGIUS, F. V.

1958. [On the scale pattern of Kamchatka sockeye of different local populations.] O stroenii cheshui Kamchatskoĭ krasnoĭ raznykh local'nykh stad. *In* Materialy po biologii morskogo perioda zhizni dal'nevostochnykh lososeĭ, pp. 52–63. Moscow, Vsesi͡uznyi Nauchno-issledovatel'skii Institut Morskogo Rybnogo Khozi͡aĭstva i Okeanografii (VNIRO). [Translation by R. E. Foerster, 10 pp. Fisheries Research Board of Canada, Translation Series No. 181.]

KROGIUS, F. V., AND E. M. KROKHIN.

1956. [Results of a study of the biology of sockeye salmon, the conditions of the stocks and the fluctuations in numbers in Kamchatka waters.] Rezulytaty issledovanii biologii nerki-krasnoĭ, sostoi͡anii͡a ee zapasov i kolebanii chislennosti v Vodakh Kamchitki. Voprosy Ikhtiologiĭ, No. 7, pp. 3–20. [Translation by R. E. Foerster, 21 pp., 1956, Fisheries Research Board of Canada, Translation Series No. 176.]

LANDRUM, B. J., AND T. DARK.

1963. Morphological classification of 1960 red salmon. International North Pacific Fisheries Commission, Annual Report, 1961, pp. 108–114.

MARGOLIS, LEO.

1963. Parasites as indicators of the geographical origin of sockeye salmon, *Onchorhynchus nerka* (Walbaum), occurring in the North Pacific Ocean and adjacent seas. International North Pacific Fisheries Commission, Bulletin No. 11, pp. 101–156.

MOSHER, KENNETH H., RAYMOND E. ANAS, AND KENNETH L. LISCOM.

1961. Study on scales. International North Pacific Fisheries Commission, Annual Report, 1960, pp. 88–95.

RIDGWAY, G. J., J. E. CUSHING, AND G. L. DURALL.

1958. Seriological differentiation of populations of sockeye salmon, *Oncorhynchus nerka.* U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 257, 9 pp.

RIDGWAY, GEORGE J., AND GEORGE W. KLONTZ.

1960. Blood types in Pacific salmon. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 324, 9 pp.

RIDGWAY, G. J., G. W. KLONTZ, AND C. MATSUMOTO.

1962. Intraspecific differences in the serum antigens of red salmon demonstrated by immunochemical methods. International North Pacific Fisheries Commission, Bulletin No. 8, pp. 1–13.

ROUNSEFELL, GEORGE A.

1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 130, vol. 58, iv+ pp. 83–169.

ROYAL, LOYD A.

1953. The effects of regulatory selectivity on the productivity of Fraser River Sockeye. The Canadian Fish Culturist, No. 14 (October), pp. 1–12.

SATO, ROKUJI.

1938. On the migratory speed of salmon and the stock of red salmon estimated from the tagging experiments in the northern North Pacific. Bulletin of the Japanese Society of Scientific Fisheries, vol. 7, No. 1, pp. 21–23. [In Japanese, with English summary. May 1938. Translation by Lorry Nakatsu, U.S. Fish and Wildlife Service, Pacific Salmon Investigations, Seattle, Wash., Translation Series No. 5.]

SATO, ROKUJI.

1939. On salmon tagging experiments in the northern North Pacific in 1937 and 1938. Bulletin of the Japanese Society of Scientific Fisheries, vol. 8, No. 4, pp. 178–184. [In Japanese, with English summary. Translation by Robert Ting, U.S. Fish and Wildlife Service, Pacific Salmon Investigations, Seattle, Wash., Translation Series No. 3.]

SEMKO, R. S.

1953. [The stocks of west Kamchatka salmon and their commercial utilization.] Zapasy zapadno kamchatskikh lososei i ikh promyslovoe ipolzovanie. Izvestiia Tikhookeanskovo Nauchno-isseledovatelskovo Instituta Rybnovo Khoziaistva; Okeangrafii (Vladivostok) (TINRO) *41*, pp. 3–109. (Translation by R. E. Foerster and L. V. Sagen, 1960, Fisheries Research Board of Canada, Translation Series No. 30.)

1961. Contemporary changes in the abundance of Pacific salmon and their fundamental causes. Sovrenennye izmeneniia chislennosti Tikhookeanskikh lososei i ikh osnovnye priohiny. *In* Trudy Soveshchaniia po dinamiko chislennosti tyb, edited by E. N. Pavlovskii, pp. 117–129. Moska, Akademiia Nauk SSR. Ikhtiologicheskaia Komissia, Trudy Soveshchanii, vyp. 13.

SIMPSON, ROBERT R.

1960. Alaska Commercial Salmon Catch Statistics 1951–1959. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Statistical Digest No. 50, 115 pp.

TAGUCHI, KISABURO.

1956. The salmon fisheries and salmon resources of the northern waters. Northern Waters Fisheries Resources Investigation Conference (Hokuyo Shigen Kenkyu KyōgiKai), 1956. 290 pp. [In Japanese, with English summary]. (Revised edition published by Nichiro Gyogyo Kabushiki Kaisha [Nichiro Fishing Co., Ltd. 1, 1957. 166 pp. In Japanese].)

1957a. The seasonal variation of the good fishing area of salmon and the movements of the water masses in the waters of Western North Pacific. II. The distribution and migration of salmon populations in offshore waters. Bulletin of the Japanese Society of Scientific Fisheries, vol. 22, No. 9, pp. 515–521. The Japanese with English summary.

1957b. The seasonal variation of the good fishing area of salmon and the movement of water masses in the waters of the Western North Pacific. III. Relation between the distribution of salmon population and oceanographical condition mainly in the southern waters of 48° N. lat. Bulletin of the Japanese Society of Scientific Fisheries, vol. 22, No. 10, pp. 609–617. The Japanese with English summary.

TAGUCHI, KISABURO, and KIYOSHI KISHIKAWA.

1954. Some knowledge on the migration of salmon in Asiatic region inferred from the data of the past. I. Red salmon (*Onchorhynchus nerka*). Bulletin of the Japanese Society of Scientific Fisheries, vol. 20, No. 7, pp. 581–585. The Japanese with English summary.

U.S. FISH and WILDLIFE SERVICE.

1946–1953. Alaska fishery and fur seal industries—1944 to 1950. U.S. Department of the Interior, Fish and Wildlife Service, Statistical Digests, Nos. 13, 15, 17, 20, 23, 26 and 29. Various pagination.

RELATION BETWEEN SPAWNING-STOCK SIZE AND YEAR-CLASS SIZE FOR THE PACIFIC SARDINE *SARDINOPS CAERULEA* (GIRARD)

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ABSTRACT

A high degree of inverse correlation between spawning-stock size and year-class size (based on indices of total fish caught) was found for the Pacific sardine (*Sardinops caerulea*). Over the 26-year period for which data are available it appears that catch, on which the indices are based, was determined primarily by population size and secondarily by availability and effort. The data indicate that spawning-stock size influences year-class size and that this is not merely a secondary result of year classes occurring in cycles which generate similar cycles of spawning populations several years later.

The object of this paper is to explore the relationships between spawning-stock size and year-class size for the Pacific sardine, *Sardinops caerulea* (Girard). It also treats to a lesser extent some of the other related factors involved in the population dynamics of the sardine.

The introductory paragraphs of Clark and Marr (1955) sum up the considerations of the problems as follows:

> At the present stage of our knowledge, there is rather universal agreement that the only way Man can affect a population of marine fishes is by fishing (and, perhaps, by pollution in special situations). That is, we cannot economically fertilize large areas of the sea, nor can we treat epidemics in fish populations, nor hope to stock the ocean by means of hatchery-reared fish. There is further agreement that Man can affect fish populations by varying the amount of fishing and by varying the method of fishing. There is, however, disagreement about the nature and magnitude of such effects.
>
> According to one theory, big spawning populations produce bigger year-classes than do small spawning populations. Therefore, one might suppose that reducing the total catch would make the spawning population bigger and therefore result in the production of bigger year-classes. Although this assumption has been made many times, it has not been demonstrated for any marine fish. The possibility that this theory does not conform to the fact will be discussed below. Unfortunately, this assumption is perhaps more often made tacitly than explicitly. There must, of course, be a critical population size below which the population will not be able to perpetuate itself.

And further:

> The death rates from fishing and from natural causes can clearly be variable and will be influenced by many factors, so that it is difficult to generalize about them. Two features are of interest, however. One of these concerns the fact that when fishing mortality is imposed on a population, natural mortality is to some extent replaced by fishing mortality. That is, some of the fish which would have died naturally during a given time interval are caught instead. The other feature, and by far the most important one, is that as far as we can judge from all the observations that have been made, fishing and natural mortality exert their greatest influence on the size of the population existing at the time they occur. Opinions differ about their effect on the size of future additions to the population, i.e., year-class which will be produced subsequent to the time the mortalities occur.
>
> There must, of course, be some "critical," minimum spawning stock size below which year-class size is a function of stock size, as we have already stated. This critical stock size has not yet been measured for any marine fishes. Above this minimum stock size all present evidence indicates that the magnitude of additions to the population (the size of individual year-classes) is not determined by the number of eggs spawned, but rather by variations in survival rate between the time the eggs are spawned and the time the resulting fish have grown large enough to enter the population. This means that the size of any particular year-class is determined, not by the number of adult fish

(above minimum) which produce it, but rather by variations in the environment which affect survival rate after the eggs are spawned.

Clark and Marr were unable to agree on whether the size of the spawning stock determined the size of the year class. Their disagreement centered on whether or not large spawning stocks produced large year classes and small spawning stocks produced small year classes. The present paper extends their data from 19 to 26 years and reexamines the problem from a different point of view.

SOURCES OF DATA

The index of spawning population size and the index of year-class size used in this paper are essentially those used by Clark and Marr (1955), which they call "accumulated age estimates." The spawning-stock size in any given season is considered to consist of all fish having scales with three or more annuli taken in the following fall-winter fishery and all fish of these year classes taken in subsequent years plus one-half of the fish having two annuli taken in the following fall-winter fishery and one-half of the fish of this year class taken in subsequent years.

The northern fishery of the earlier years was actually a summer-fall fishery, and the expanded Mexican fishery of more recent years is pursued throughout the year although the heaviest landings generally coincide with the southern California fall fishery.

Estimates of a year class are derived by summing all fish of that year class caught during its life span with the following exceptions: only one-half of the fish with one annulus and one-fourth of the fish with no annuli are included. Fish in their first year were seldom taken by the commercial fishery, and fish with only one annulus were taken in appreciable quantities in only a few years. Most of the commercial sardine catch is made up of 2- and 3-annulus fish.

The above measure of spawning-stock size is used because it is the same as that used by Clark and Marr (1955). Actually age at first spawning varies over the geographic range of the sardine, apparently occurring earlier in the south and later in the north; it also varies from year to year. Also if the spawning-stock size is considered to be either all fish 2 years old or older or all fish 3 years old or older, and if the year class either includes or excludes fish taken at less than 2 years of age, the correlations obtained between year-class size and spawning-stock size are as good as those obtained from the measurements used in this paper.

The age composition of the commercial sardine catch was obtained from the following sources:

Year:	*Author*
1932 through 1937–38	Eckles (1954).
1938–39 through 1940–41	Wolf (1961).
1941–42 through 1946–47	Felin and Phillips (1948).
1947–48	Mosher et al. (1949).
1948–49 through 1955–56	Felin et al. (1949, 1950, 1951, 1952, 1953, 1954, 1955, 1958).
1956–57	Wolf et al. (1958).
1957–58	Daugherty and Wolf (1960).
1958–59	Wolf and Daugherty (1961).

Data for the 1959–60 and 1960–61 seasons were made available by Robert Wolf of the Bureau of Commercial Fisheries, and data for the Mexican fishery not already in the above reports by Makoto Kimura also of the Bureau of Commercial Fisheries. The only data available for some ports in a few of the earlier years are tons landed. These have been converted to age and numbers of fish on the basis of known age compositions of landings at the nearest ports having similar age composition landings in other years.

ANALYSIS OF DATA

The magnitude of the commercial catch depends upon 1) sardine population size, 2) fishing effort, and 3) availability of sardines to the fishing fleet. Over the 26-year period covered by this paper, the population size is the primary factor determining catch. Effort and availability may be considered as sampling errors whose effect is not great enough to negate the use of an index of population size based on catch. During the early years covered by the data, effort was increasing. This would cause earlier estimates of population size and year-class size to be lower with the latter less underestimated because of the 2-year lag. During the late 1940's to the present there have been first considerable fluctuation in fishing effort and finally a decrease in effort, both of which appear to be primarily responses to population size (as measured by catch) in the immediately preceding fishing seasons.

Although the range of the sardine has contracted considerably, and these fish are no longer available in commercial quantities in the northern portions of their former range, the sardine population still shifts northward in the summer and southward in the winter.

The population as a whole has shown fluctuations in availability as evidenced by changes in total mortality rates from year to year. In some years all year classes in the catch show a negative total mortality which cannot be accounted for by increased effort. This must result from increased availability. The seasonal shifts in sardine population do not seem to be constant from year to year, and consequently availability has its greatest effect in the most northern portion of the range.

The method of accumulating ages tends to offset the errors of changing effort and availability but not as much as it would in a longer lived species of fish. Changes in both availability and effort undoubtedly account for some of the variation in the correlations between spawning-stock size and year-class size.

Direct correlation methods are usually applied to frequency series rather than time series unless, in the latter case, neither of the time series is marked by a definite secular trend. The direct correlation of time series data can easily give a fortuitously high correlation. One method of circumventing this difficulty is to determine trends for the data and correlate the deviations from the trends. This method applies only when the parameters involved react to one another relative to their trends, rather than absolutely without regard to trends.

A third degree parabolic trend line, $Y_c=5.079+0.5475X-0.06670X^2+0.001497X^3$, in which Y_c =calculated spawning-stock size index in billions of fish and X=trend year, was fitted to the spawning-stock size indices (fig. 1). Similarly a third degree parabolic trend line, $Y_c=2.463+0.6050X-0.06754X^2+0.001614X^3$, in which Y_c=calculated year class size index in billions of fish and X=trend year was fitted to the year-class size indices (fig. 2).

The deviations of the observed values from calculated values were obtained. These data are presented in table 1. In figure 3 the two sets of deviations are plotted as anomalies from their trends. Year-class size deviations are plotted against spawning-stock size deviations in figure 4. The least squares regression line $Y_c=0.000136-0.6774X$ is also plotted. The correlation coefficient, r, equals -0.699, with a probability that such a correlation could be obtained by chance alone of less than one in a thousand.

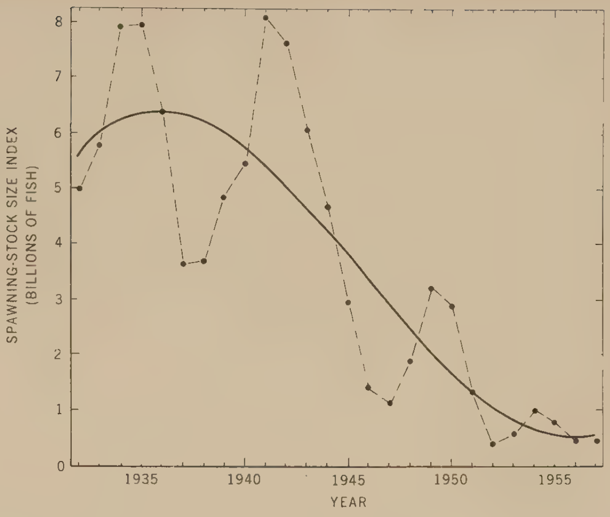

FIGURE 1.—Apparent trend of sardine spawning-stock size index, 1932–57.

As stated above the method of correlating deviations from trend guards against spuriously high correlations that may be obtained if trend data are directly correlated. In the present case the fact that two sets of parameters having such closely coincident trends do not have a high direct positive correlation is in itself significant. As we have seen this is caused by the fact that the parameters are inversely related with respect to trend.

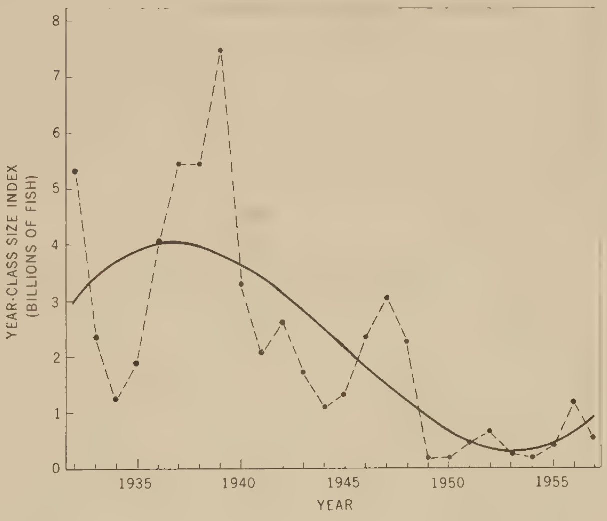

FIGURE 2.—Apparent trend of sardine year-class size index, 1932–57.

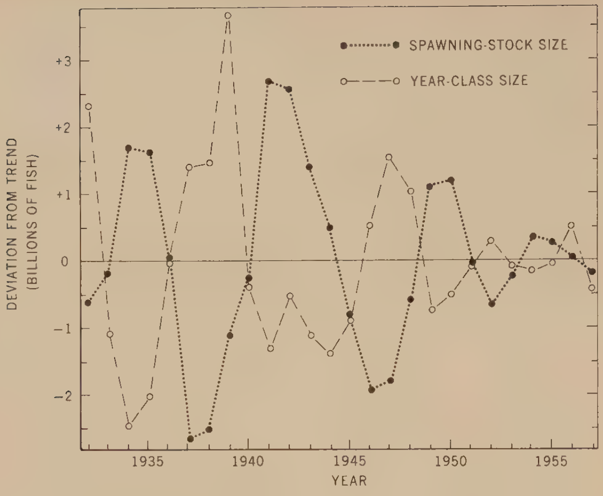

FIGURE 3.—Deviations from trends of sardine spawning-stock size index and year-class size index, 1932–57.

TABLE 1.—*Indices of spawning-stock size and year-class size of the Pacific sardine. Observed and computed values and deviations*

[Billions of fish]

Year	Trend year	Spawning-stock size			Year-class size		
		Observed	Calculated	Deviation	Observed	Calculated	Deviation
1932	1	4.96	5.56	−0.60	5.33	3.00	2.33
1933	2	5.76	5.92	−.16	2.37	3.42	−1.05
1934	3	7.87	6.16	1.71	1.26	3.71	−2.45
1935	4	7.94	6.31	1.63	1.89	3.91	−2.02
1936	5	6.34	6.34	.00	4.03	4.00	.03
1937	6	3.64	6.29	−2.65	5.44	4.01	1.43
1938	7	3.67	6.16	−2.49	5.42	3.94	1.48
1939	8	4.83	5.96	−1.13	7.47	3.81	3.66
1940	9	5.44	5.70	−.26	3.27	3.61	−.34
1941	10	8.09	5.38	2.71	2.07	3.37	−1.30
1942	11	7.61	5.02	2.59	2.59	3.10	−.51
1943	12	6.04	4.63	1.41	1.69	2.79	−1.10
1944	13	4.69	4.22	.47	1.07	2.46	−1,39
1945	14	2.95	3.78	−.83	1.27	2.13	−.86
1946	15	1.39	3.34	−1.95	2.32	1.79	.53
1947	16	1.11	2.90	−1.79	3.03	1.47	1.56
1948	17	1.88	2.47	−.59	2.22	1.16	1.06
1949	18	3.18	2.06	1.12	.14	.89	−.75
1950	19	2.89	1.68	1.21	.15	.65	−.50
1951	20	1.31	1.33	−.02	.41	.46	−.05
1952	21	.39	1.03	−.64	.63	.33	.30
1953	22	.58	.79	−.21	.22	.27	−.05
1954	23	.97	.61	.36	.16	.29	−.13
1955	24	.78	.50	.28	.36	.40	−.04
1956	25	.43	.48	.05	1.16	.60	.56
1957	26	.41	.55	−.14	.52	.91	−.39

As also stated above, the trend method cannot be applied to parameters that react to one another absolutely, which is generally the case when biological parameters are involved. In fact, one would expect this to be the case in the present instance. As will be shown later, the period of years involved may be divided into three more or less distinct phases of population contraction. The same phenomena of population dynamics seem to be functioning within successively smaller population ranges. This permits the population data to be treated as a trend that allows the data for all years to be included in a single correlation.

By using the trend method, the total fish caught spawning-stock size index may be compared to a second, more frequently used population size index, catch per unit of effort. Such data are available for 23 seasons for the California fishery from 1932–33 through 1954–55 (Marr, 1960).

Catch per unit of effort data (tons of sardines landed per boat-month) are presented in table 2. A third degree parabolic trend line ($Y_c=693.76-28.854X-0.034874X^2-0.0047127X^3$ in which Y_c= computed catch per unit of effort and X=trend year) was fitted to these data (fig. 5). When the deviations from trend of spawning-stock size index are correlated with the deviations from trend of catch per unit of effort for the 23 seasons, a positive correlation coefficient of 0.822 is obtained. The data were fitted to the least squares regression line, $Y_c=-0.0057656+0.011304X$, in which Y_c=computed spawning stock size deviation and X=catch per unit of effort deviation (fig. 6).

There is no reason to believe that catch per unit of effort is necessarily a better measure of

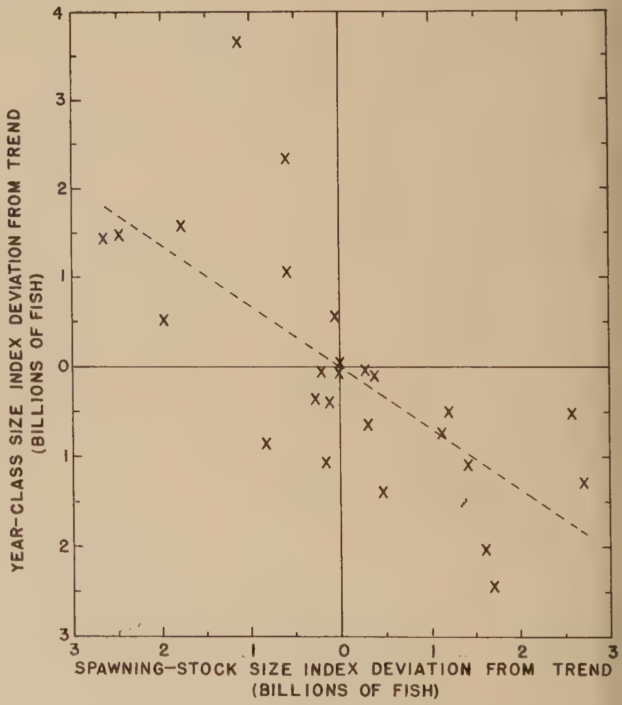

FIGURE 4.—Deviation from trend of year-class size plotted against deviation from trend of spawning-stock size for 26 years (1932–57).

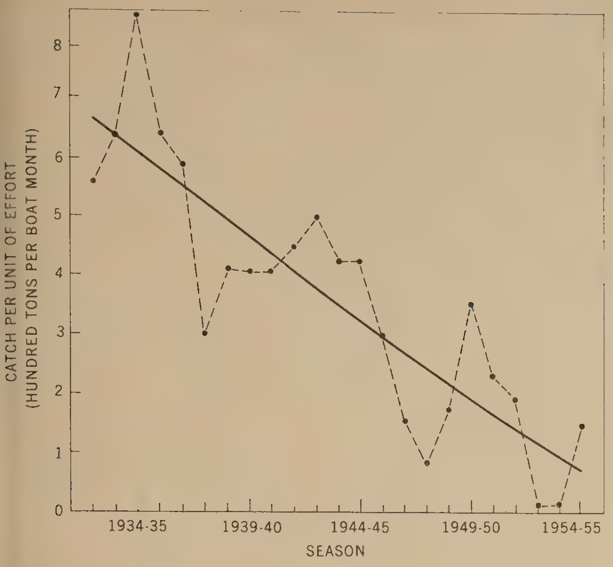

Figure 5.—Apparent trend of sardine catch per unit of effort, 1932–33 through 1954–55 seasons.

population size than the total fish caught index. The former accounts for changing effort but measures only the population available to the fishery in that year. The latter tends to average the effects of both effort and availability over several years. At relatively low levels of fishing effort directed against a stable fish population one might reasonably expect that changes in effort would result in directly proportional changes in catch. However, at relatively high levels of fishing effort a "saturation point" is reached above which relatively large changes in effort result in relatively small changes in catch. This effort saturation point seems to have been exceeded throughout most of the period covered in this paper as later data will indicate. The above conditions will tend to impair the accuracy of the catch per unit of effort index to a greater extent than the total fish caught index. The excellent correlation between the two indices, however, is evidence of their validity as measures of population size.

Table 2.—*Observed and calculated California catch per unit of effort data (tons per boat-month) and deviations compared with spawning-stock size index deviations*

Year	Trend year	Observed catch per unit of effort	Computed catch per unit of effort	Deviation	Spawning-stock size index deviation
932–33	1	557	665	−108	−0.60
933–34	2	636	636	0	−.16
934–35	3	835	607	228	1.71
935–36	4	638	578	60	1.63
936–37	5	586	549	37	.00
937–38	6	302	520	−218	−2.65
938–39	7	409	492	−83	−2.49
939–40	8	405	463	−58	−1.13
940–41	9	404	435	−31	−.26
941–42	10	447	406	41	2.71
942–43	11	497	378	119	2.59
943–44	12	422	351	71	1.41
944–45	13	420	323	97	.47
945–46	14	302	296	6	.83
946–47	15	153	269	−116	−1.95
947–48	16	81	242	−161	−1.79
948–49	17	173	216	−43	−.59
949–50	18	352	191	161	1.12
950–51	19	229	165	64	1.21
951–52	20	187	140	47	−.02
952–53	21	10	116	−106	−.64
953–54	22	11	92	−81	−.21
954–55	23	145	69	76	.36

Another method of demonstrating the relation between year-class size and spawning-stock size (fig. 7) involves fitting a parabola directly to the data. Ricker (1954) gives a number of examples of reproduction curves of somewhat similar nature. The curve I have fitted in figure 7 is a transformation of the straight line fitted to recruits per spawner plotted against spawning-stock size. That is, if Y equals year-class size and X equals spawning-stock size, a straight line may be fitted to $\frac{Y}{X}=1.28867-0.12658X$. Multiplying through by X gives a second degree parabola: $Y=1.28867X$

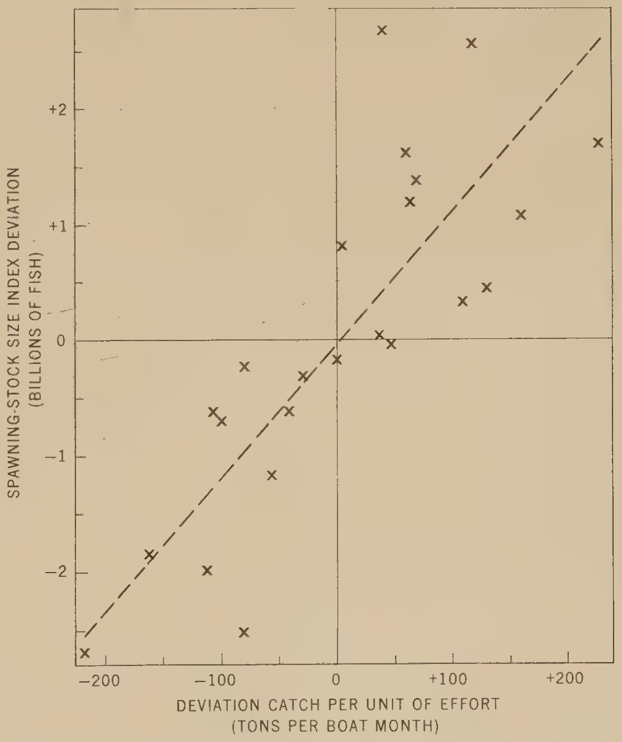

Figure 6.—Deviation from trend of spawning-stock size plotted against deviation from trend of catch per unit of effort for 23 seasons (1932–33 through 1954–55).

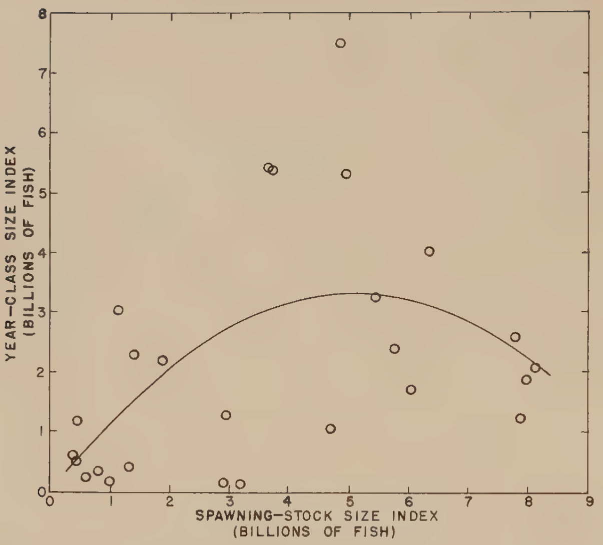

Figure 7.—Sardine year-class size plotted against spawning-stock size with fitted second degree parabola, $Y=1.28867X-0.12658X^2$, $r=0.539$, $p<.01$.

$-0.12658X^2$. A straight line may be fitted to random numbers as above and will yield a significant correlation if enough pairs of random numbers are used, but the transformation of such a line will, of course, no longer show a significant correlation.

In figure 8 spawning-stock size and year-class size indices are plotted against time for the sardine data. In figure 9 the observed spawning-stock size index and the computed values for year-class size obtained from the curve in figure 7 are plotted against time. A comparison of these two figures indicates that the curve is not an adequate description of the data. It is difficult to see how this curve would describe such a relationship when the fish species is fairly short-lived, year-class size is measured after the fish enters the fishery, and the data follow a somewhat cyclical pattern. In order for the population to pass over from the right limb of the curve to the left limb, it would have to move through a period of large year-class production which would throw it back to the right limb again.

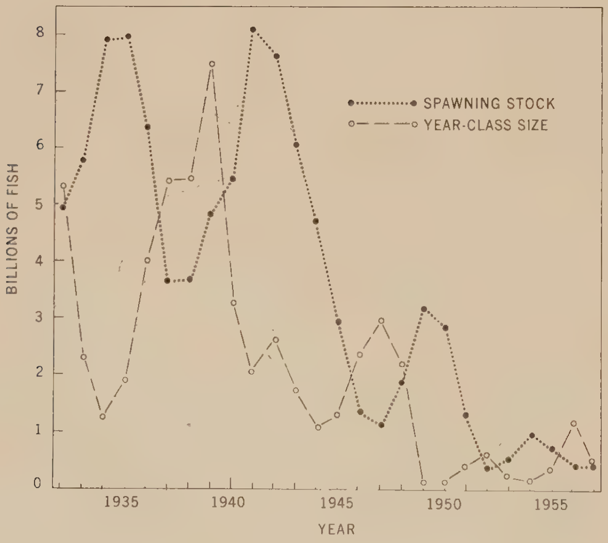

Figure 8.—Sardine year-class size and spawning-stock size plotted against time, 1932–57.

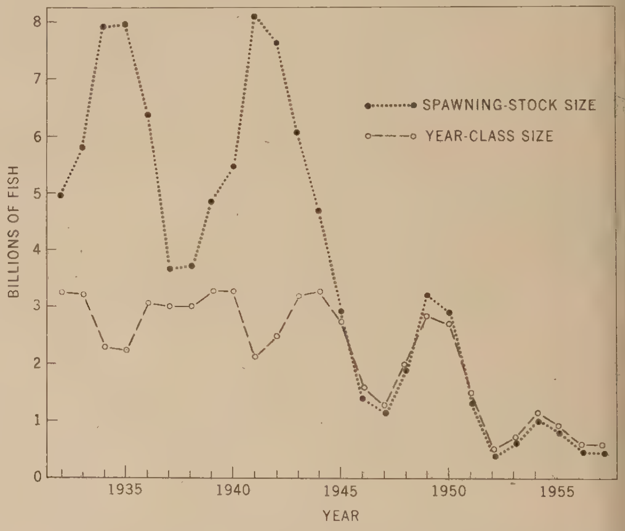

Figure 9.—Sardine year-class size index computed from curve (fig. 7) and observed spawning-stock size index plotted against time (1932–57).

Although the method of analyzing the data by trend deviation is satisfactory for the entire period covered, a more illuminating analysis may be obtained by breaking the data down into three periods of no trend which may be treated separately. The data are presented in this manner in figure 10. The straight line on the right is fitted to the data for the 11 years 1932–42; the line in the middle is fitted to the 6 years 1945–50; and the line on the left is fitted to the 6 years 1952–57. The years 1943 and 1944 marked the beginning of the first collapse of the fishery. Both of these collapses were associated with reductions in the range of the sardine. In the mid-1940's the sardine disappeared in commercial quantities from British Columbia to Central California and the Central California fishery became sporadic. The

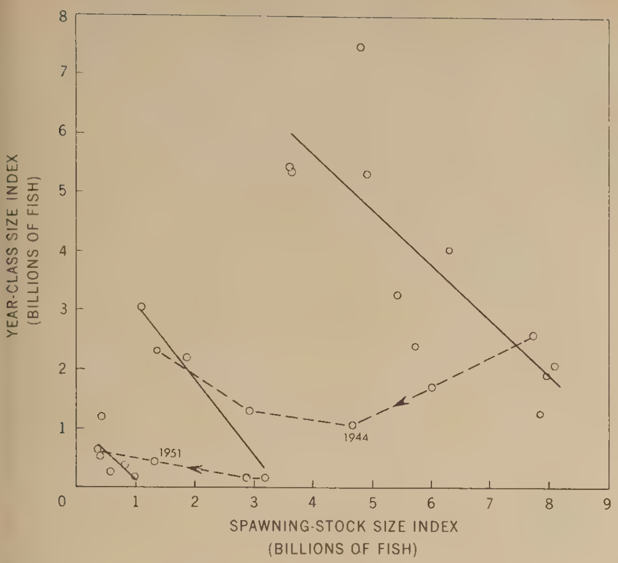

Figure 10.—Sardine year-class size index plotted against spawning-stock size index and lines fitted to each of the three periods 1932–43, 1945–50 and 1952–57.

San Pedro fishery remained relatively unaffected. In the early 1950's the Central California landings became negligible or absent and the San Pedro fishery became sporadic. It appears, however, that the same inverse relationship between spawning-stock size and year-class size persisted but within reduced ranges.

In figure 11 spawning-stock size and year-class size indices based on San Pedro landings only are plotted against time. Two fishery periods and one collapse are evident here. In figure 12 a straight line has been fitted to the 19-year period 1932–50 on the right, and a second straight line to the 7-year period 1952–58 on the left.

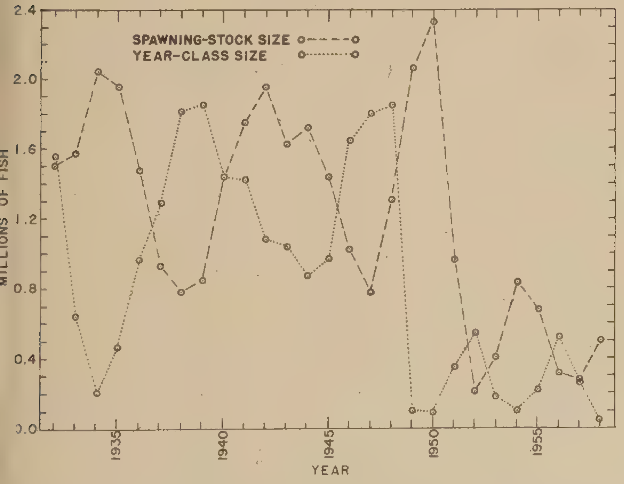

Figure 11.—Sardine year-class size index and spawning-stock size index plotted against time (1932–57) San Pedro, California, only.

The three fitted lines ($Y=a+bX$) for all ports and the two for San Pedro are presented in figure 13. Correlation data for these lines are presented in table 3. It is noteworthy that the regression lines all have about the same slope and that the periods of fishery collapse originate and cross over from the lower right-hand area of the regression lines rather than going "over a curve."

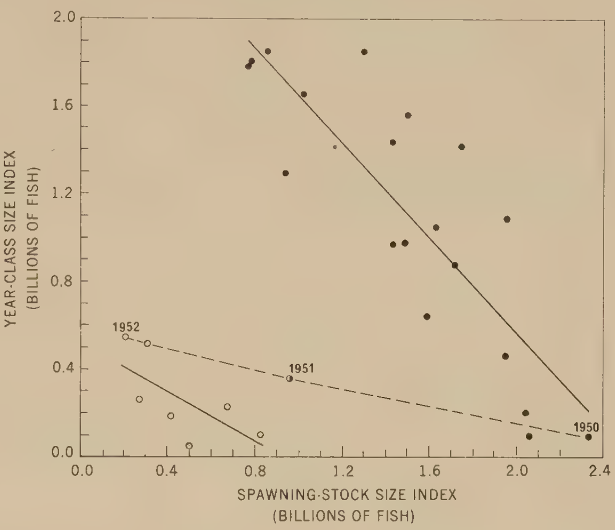

Figure 12.—Sardine year-class size index plotted against spawning-stock size index and lines fitted to each of two periods, 1932–50 and 1952–58, San Pedro only.

Table 3.—*Correlation between spawning-stock size and year-class size*

	N	r	P
Index based on—			
All ports:			
1932–42	11	−0.820	0.001
1945–50	6	−.936	.01
1952–57	6	−.669	.1
San Pedro:			
1932–50	19	−.845	.001
1952–58	7	−.691	.1

The existence of good correlations between spawning-stock size and year-class size does not in itself mean that spawning-stock size necessarily affects year-class size. On the other hand it is axiomatic that year-class size (as measured after the fish have entered the fishery or spawning stock) affects spawning-stock size a few years later. By using the method of correlating deviations from trend, an excellent negative correlation

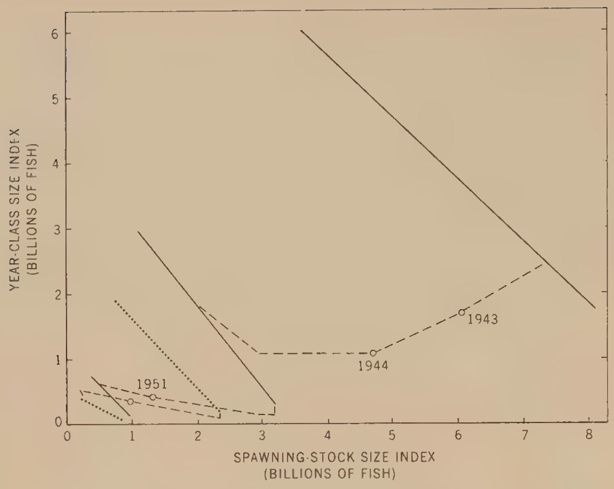

FIGURE 13.—Comparison of computed lines for three periods shown in figure 10 (all ports) and two periods shown in figure 12 (San Pedro) with transitional years plotted.

was found between spawning-stock size and year-class size. A slightly better positive correlation, however, may be found between year-class size and spawning-stock size 3 years later. Correlation coefficients of year-class size on spawning-stock size for a series of lagged and advanced years are presented in figure 14.

From the above we may hypothesize either 1) that the apparent cause and effect relationship between spawning-stock size and year-class size is merely a byproduct of the known effect of year-class size on subsequent spawning-stock or 2) that spawning-stock size actually determines year-class size. If the former is true, year-class size could either fluctuate or follow cycles. If the latter is true, year-class size would follow a cycle. Examination of the data reveals that they do appear to follow a cyclical pattern, and, in fact, if they did not, the excellent negative correlation between spawning-stock size and year-class size could not be found. Also this correlation would not result unless the length of the cycle was approximately twice the mean age of the spawning stock.

Therefore, although the effect of year-class size on subsequent spawning-stock size could cause the apparent relationship between spawning-stock size and year-class size, the circumstances under which this could occur are limited. If this hypothesis were true the factors determining year-class size would have to occur in cycles approximately equal to twice the mean age of the spawning stock. At present, the only known factor that follows this pattern is spawning-stock size.

Figure 15 presents eight population models based on the sardine data. These models illustrate what correlations would exist between spawning-stock size and year-class size if there were no cause and effect relationship between these two parameters and if the correlation resulted from the cause and effect relationship between year-class size and subsequent spawning-stock size alone. Figure 15 shows that the length of cycle determines whether or not the cycles are in or out of phase and consequently the degree and direction of the correlation. These data are presented in somewhat different form in figure 16 to which the plot of the observed correlation coefficient has been added. The factors controlling the cyclical pattern of year-class size would have to vary in approximately an 8- to 10-year cycle in order for the high observed correlation coefficient to obtain. No environmental factor varying in such a manner has yet been found.

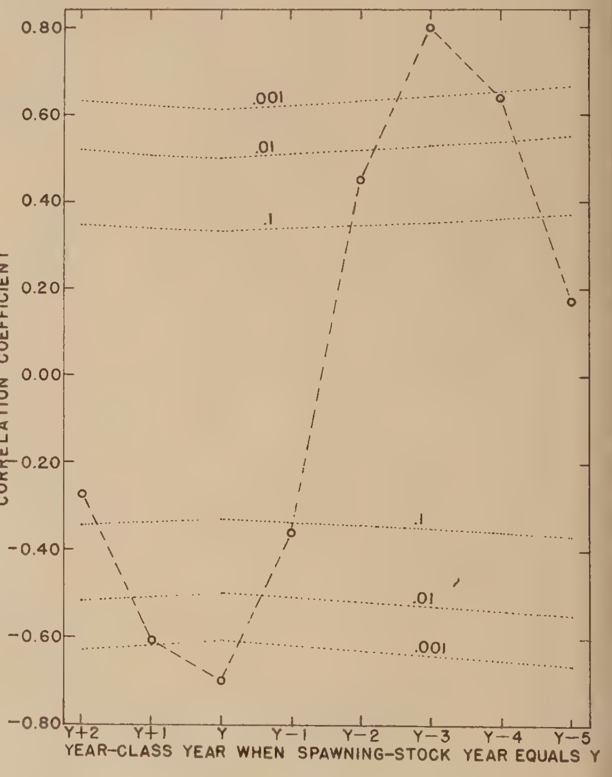

FIGURE 14.—Correlations between year-class size index deviations from trend in year, y, each of the 2 succeeding years and each of the 5 preceding years and spawning-stock size index deviations from trend in year, y.

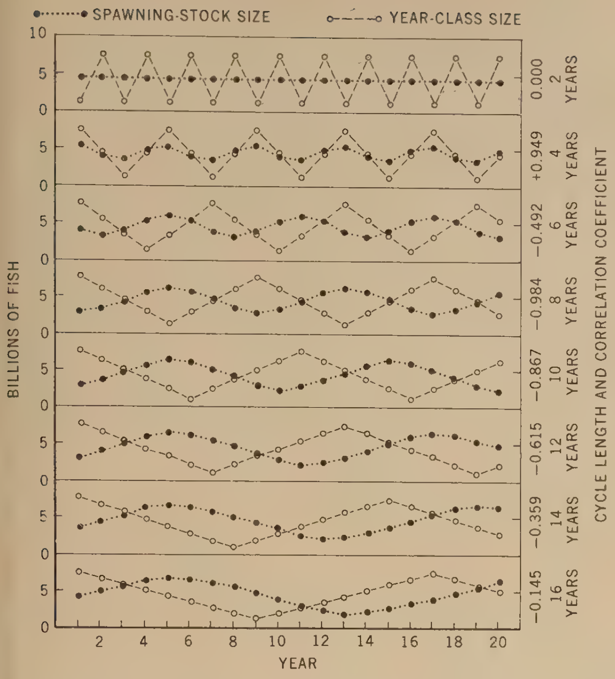

FIGURE 15.—Population models (based on sardine data) illustrating the effect (for eight cycles of different lengths) of year class strength on subsequent spawning stock size when spawning stock size exercises no influence on year-class size.

On the other hand, if spawning-stock size causes year-class size, Ricker (1954) has pointed out that the length of the cycle should be twice the mean length of a generation (interval from egg to egg). This appears to be applicable to the present data. In fact there is a shortening of the cycle length over the period covered coincident with a decrease in the mean age of spawning stocks resulting from the disappearance of the longer lived later maturing northern fish.

If it is assumed that spawning-stock size alone causes year-class size the population model, based on the sardine data, shown in figure 17 would prevail. Starting with the largest observed spawning-stock size index spawning-stock size and year-class size would fluctuate inversely in cycles of constant length but decreasing amplitude until, after many years, an equilibrium population was attained. Any environmental factors that affected the spawning-stock composition would, of course, once again initiate the fluctuating cycles.

Data comparable to those presented for the sardine may be found for the haddock (Herrington, 1948). Catch per unit of effort indices for haddock

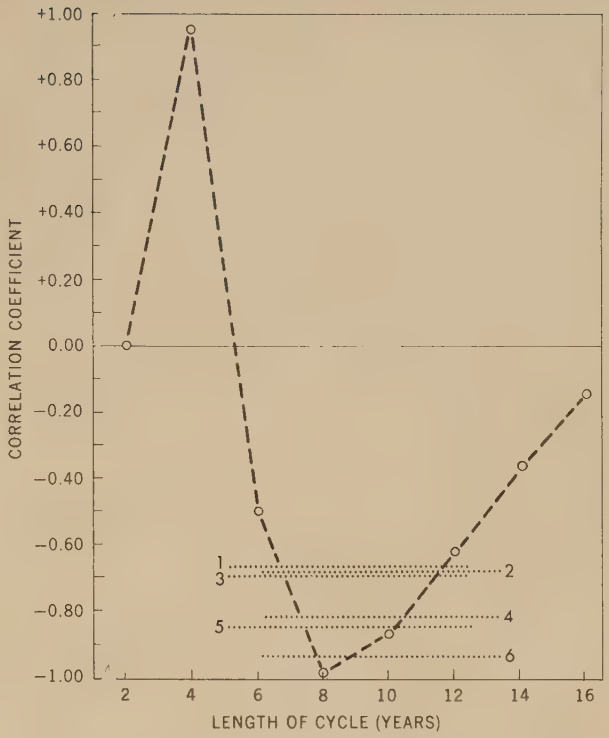

FIGURE 16.—Correlation coefficients plotted against length of cycle for data in figure 15. Observed correlation coefficients for spawning stock size index and year class size index indicated by dotted lines: No. 1 all ports 1952–57, No. 2 San Pedro 1952–58, No. 3 all ports 1932–57 (deviations from trend), No. 4 all ports 1933–42, No. 5 San Pedro 1932–50, No. 6 all ports 1945–50.

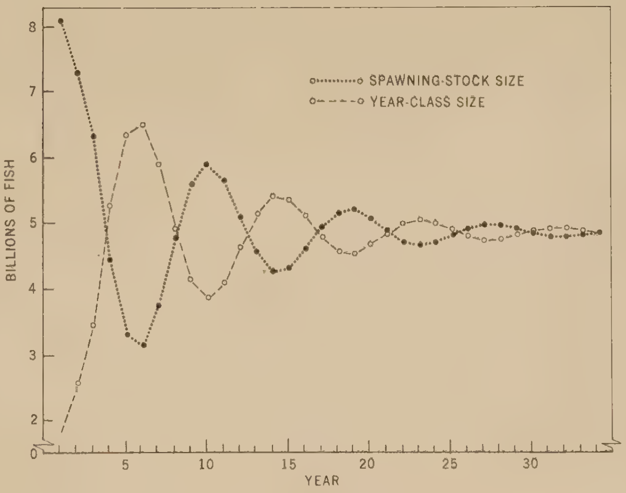

FIGURE 17.—Population models (based on sardine data) illustrating the effect of spawning-stock size on year-class size when spawning stock size determines year class size according to the straight line formula determined for sardines for all ports, 1932–43.

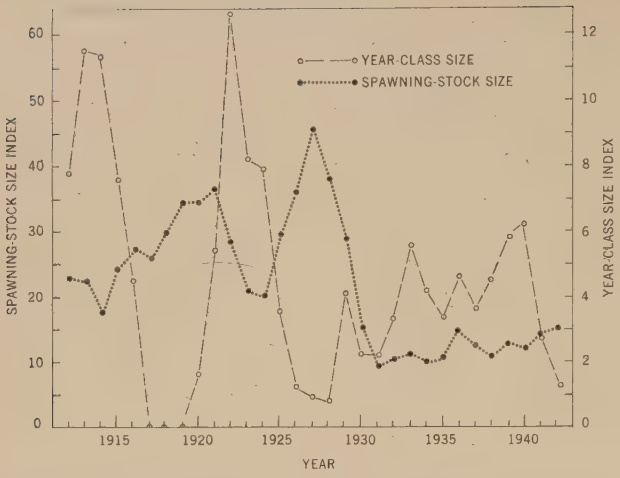

Figure 18.—Haddock spawning stock size index and year class size index plotted against time.

spawning-stock size and year-class size plotted against time are shown in figure 18. According to Ricker (1954) there was a radical change in fishing methods about 1930. The good inverse correlation between spawning-stock size and year-class size that prevailed until 1929 is no longer apparent after that date (figs. 18 and 19). The haddock has not undergone any great reduction of range comparable to that exhibited by the sardine.

The use of spawning-stock size and year-class size indices assumes that total sardines caught adequately reflects the actual population size and year-class size present in the ocean. Although this certainly appears to be true in the case of the sardine, there are several other factors that may cause some error in the estimates. One of these is effort.

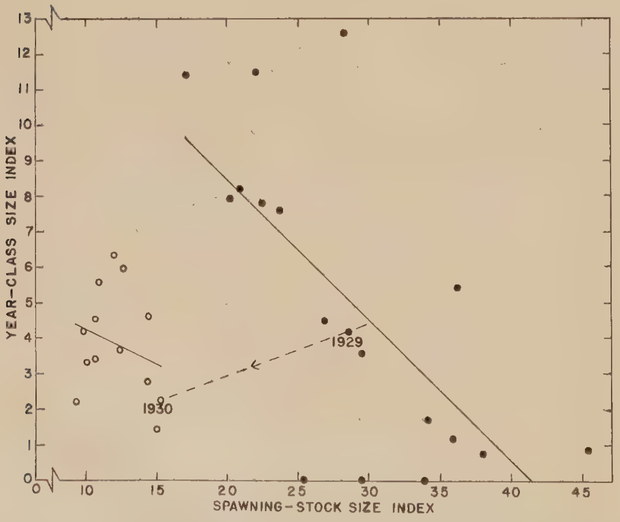

Figure 19.—Haddock year-class size index plotted against spawning-stock size index and computed regression lines for two periods (1912–29 and 1930–42).

California catch (thousands of tons) and effort (boat months) (Marr, 1960) are plotted in figure 20 and also presented in table 4.

When these values are directly correlated a correlation coefficient of 0.533 ($P.=0.01$) is obtained. However, if catch is correlated with effort 1, 2, or 3 years later, even higher correlations are obtained as follows:

Catch year	*Effort year*	*Years*	*r*
y	$y-1$	22	0. 172
y	y	23	. 533
y	$y+1$	22	. 631
y	$y+2$	21	. 636
y	$y+3$	20	. 538
y	$y+4$	19	. 419

These data are plotted with levels of probability in figure 21.

The above correlations appear to be caused at least in part by trend. Third degree parabolas were fitted to catch and effort data, and deviations obtained. These deviations are plotted for the 23 years in figure 22. The coefficient of correlation and the rank coefficient of correlation for various lagged and advanced series of years are as follows:

Catch year	*Effort year*	*Years*	*r*	*Pr*
y	$y-2$	21	-------	−0. 472
y	$y-1$	22	−0. 366	−. 570
y	y	23	. 208	. 081
y	$y+1$	22	. 197	. 206
y	$y+2$	21	. 106	. 221
y	$y+3$	20	-------	. 178

These data are plotted with levels of probability in figure 23. The great deviation in effort in the 1950–51 season tends to depress the correlation coefficients especially those of effort years $y+1$ and $y+2$ of trend deviations. The effort peaks also seem to follow the catch peaks in the earlier years and more nearly coincide with them in latter years. If the deviations from trend are correlated directly for the 1932–33 through 1948–

TABLE 4.—*California sardine catch and effort 1932–33 through 1954–55*

Season	Catch	Effort
	Thousands of tons	*Boat months*
1932–33	248	447
1933–34	382	600
1934–35	597	715
1935–36	557	874
1936–37	724	1, 236
1937–38	413	1, 368
1938–39	572	1, 401
1939–40	531	1, 312
1940–41	455	1, 125
1941–42	584	1, 306
1942–43	505	1, 008
1943–44	479	1, 123
1944–45	555	1, 304
1945–46	404	1, 313
1946–47	234	1, 487
1947–48	121	1, 356
1948–49	184	918
1949–50	334	948
1950–51	351	1, 531
1951–52	127	594
1952–53	4	466
1953–54	3	296
1954–55	66	458

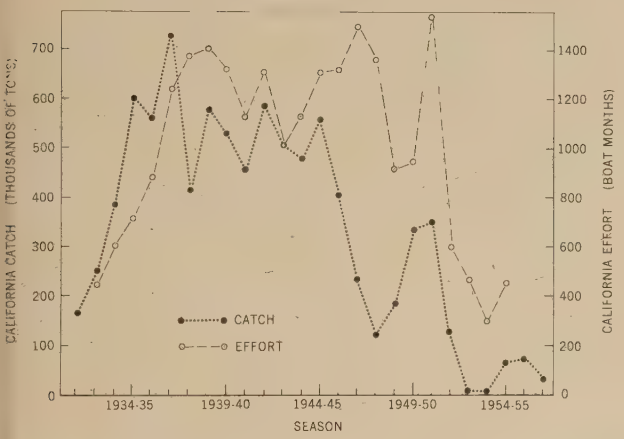

FIGURE 20.—California catch and effort plotted against time for 23 seasons.

49 period only, the following correlation coefficients are obtained:

Catch year	*Effort year*	*Years*	*r*
y	$y-3$	14	−0. 062
y	$y-2$	15	—. 434
y	$y-1$	16	—. 618
y	y	17	—. 171
y	$y+1$	16	. 117
y	$y+2$	15	. 618
y	$y+3$	14	. 569

These data are plotted with levels of probability in figure 24.

The above analysis of catch and effort data indicates that catch causes effort rather than vice versa. The lag in effort appears to be more nearly 3 years at the beginning of the period and closer to 1 year at the end of the period. It is especially noticeable also that toward the end of the period effort is low in some years because of the scarcity of fish in those same years. When preseason evidence indicates a scarcity of fish, many boats will not begin to fish and others will stop fishing within the first month or two of the season; and conversely, when fish are abundant, effort will remain high throughout the season.

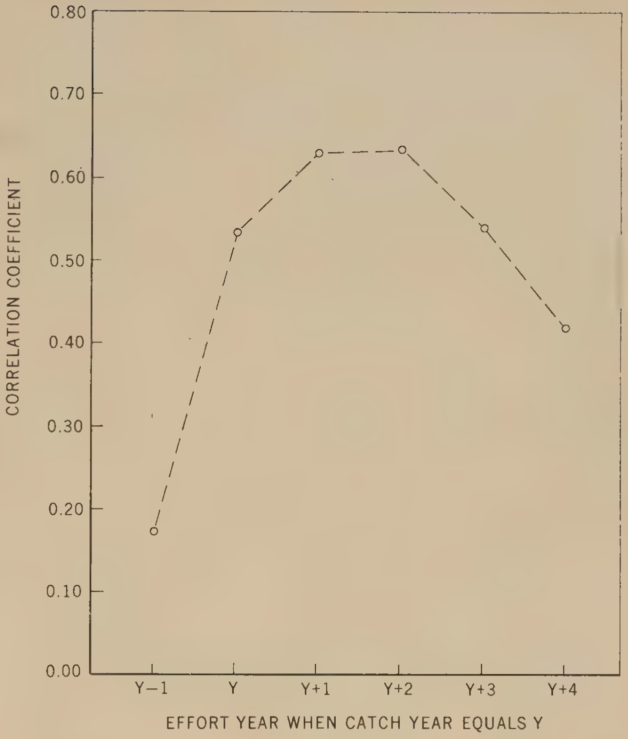

FIGURE 21.—Correlations between California catch in year, *y*, and effort in year, *y*, the preceding year, and the 4 subsequent years.

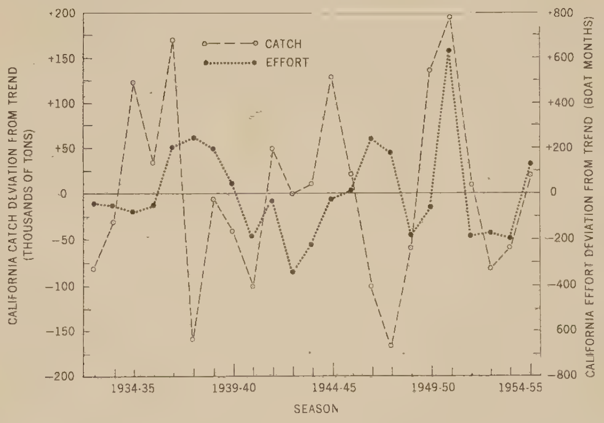

FIGURE 22.—Deviations from trend of California catch and effort, 1932–33 through 1954–55 seasons.

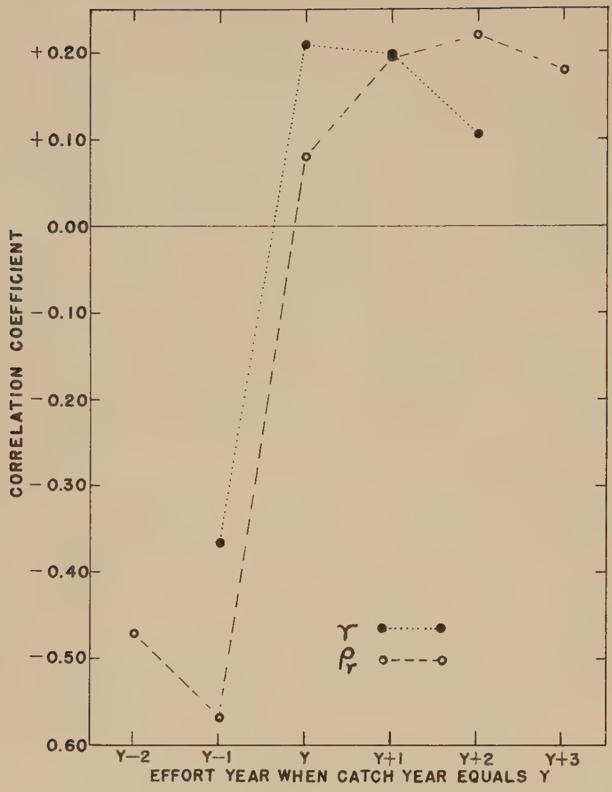

FIGURE 23.—Correlation and rank correlation between deviations from trend of California catch and effort 1932–33 through 1954–55 seasons.

It is also noteworthy that the 1934–35 effort of 715 boat-months yielded the second highest catch of the 23-year period despite the fact that effort did not drop below the 1934–35 figure until 1951–52 and averaged 54 percent higher during these 16 years. The high negative correlations between effort in one year and catch the following year may mean that high effort in one year will reduce the catch in the following year or it may only be a manifestation of the cyclical nature of the data.

Two-annulus sardines are not fully available to the fishery. This may be seen from the following 28-year average (geometric mean) survival rates for sardines based on all ports:

Percent	*From annuli—*	*to annuli—*
109	2	3
46	3	4
37	4	5
30	5	6
22	6	7
10	7	8

A survival rate of 109 percent would be impossible if the fishery sampled the 2-annulus fish equally as well as the older fish. There may also be some selectivity of larger fish by fishermen.

Table 5 presents correlation coefficients obtained from direct correlations of various pairs of parameters based on the San Pedro sardine fishery for the 14-year period 1937–38 and 1950–51. These parameters exhibit negligible trend over this period.

TABLE 5.—Correlation coefficients[1] for various pairs of parameters, San Pedro sardines 1937–38 through 1950–51 seasons

	Spawning-stock size index	Effort	Catch
Percent of year class taken as 2-annulus fish	−0.773	−0.007	+0.137
Effort	−.342		+.309
Spawning-stock size index		−.342	−.031

[1] Probability levels: N=14 $n=12$ $P=0.1$ 0.01 0.001
$r=0.458$ .661 .780

There is an excellent negative correlation between spawning stock size index and the percent of a year class taken as 2-annulus fish. None of the other pairs of parameters involved yields a significant correlation for this period of years.

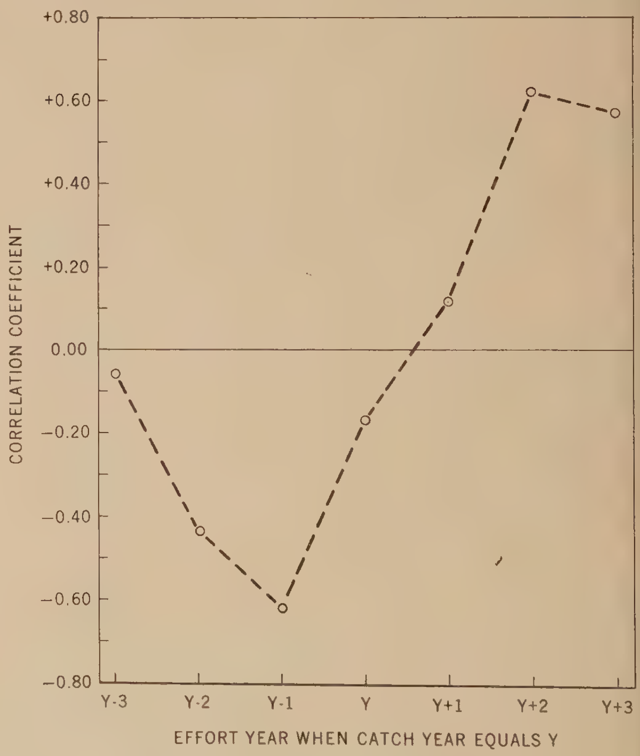

FIGURE 24.—Correlations between deviations from trend of California catch in year, *y*, and effort deviations from trend in year, *y*, the preceding 3 years and the succeeding 3 years.

These data indicate that catch was maintained relatively high during periods of low spawning-stock size by directing more fishing effort against the 2-annulus fish which were entering the fishery at that time.

A measure of survival or mortality may be obtained by comparing the number of sardines having three or more annuli caught in one season with the number of sardines having four or more annuli caught in the following season. This measure includes the effect of changing effort and availability. This is shown by the fact that in some years survivals in excess of 100 percent (or negative mortalities) may be obtained.

Survival data, computed as above, are presented in table 6 and figure 25 for all ports and for San Pedro only. Logarithmic second degree parabolic trend line values fitted to these data are also plotted. The apparent high survival values during 3 of the first 4 years are probably caused by increasing effort as the fishery was developing. Following that period, effort appears to be saturated with respect to population size and its effects become secondary. In theory effort should affect survival rates both absolutely and relatively. A high effort should increase total mortality thus decreasing survival, and a low effort should conversely increase survival. Also a change from a lower effort to a higher effort should cause apparent survival to increase. These relationships are not apparent in the survival data.

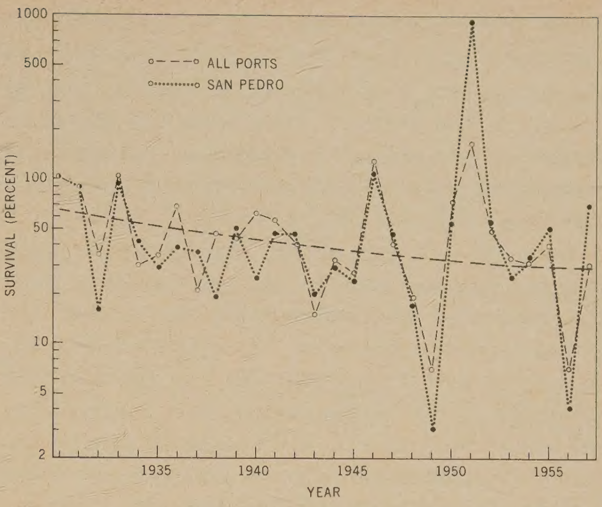

Figure 25.—Apparent survival trends for all ports and San Pedro only, 1933 through 1960.

In addition to being affected by the increasing effort during the early years, the trend lines are also influenced by the changing age composition of the population. In the earlier years a greater proportion of the population was made up of the

Table 6.—*Sardine survival as measured by 4-annulus and older fish caught in one year expressed as a percent of 3-annulus and older fish caught the preceding year*

Season		All ports				San Pedro			
		Population size (millions of fish)		Survival (percent)		Population size (millions of fish)		Survival (percent)	
3-annulus and older	4-annulus and older	3-annulus and older	4-annulus and older	Observed	Computed	3-annulus and older	4-annulus and older	Observed	Computed
1932–33	1933–34	1,401	1,459	104	65.1	473	489	103	56.1
1933–34	1934–35	1,769	1,532	87	62.1	578	509	88	52.9
1934–35	1935–36	2,807	981	35	59.3	877	142	16	50.0
1935–36	1936–37	2,829	2,918	103	56.7	719	678	94	47.4
1936–37	1937–38	3,861	1,151	30	54.3	861	369	43	45.1
1937–38	1938–39	1,672	645	39	52,0	510	149	29	43.1
1938–39	1939–40	890	604	68	50.0	206	78	38	41.3
1939–40	1940–41	1,875	399	21	48.0	244	88	36	39.7
1940–41	1941–42	1,544	799	47	46.2	409	78	19	38.4
1941–42	1942–43	2,378	1,075	45	44.6	543	269	50	37.2
1942–43	1943–44	2,981	1,862	62	43.1	941	237	25	36.1
1943–44	1944–45	2,893	1,627	56	41.6	587	276	47	35.2
1944–45	1945–46	2,384	948	40	40.3	797	370	46	34.5
1945–46	1946–47	1,819	270	15	39.1	740	151	20	33.9
1946–47	1947–48	654	210	32	37.9	471	137	29	33.4
1947–48	1948–49	404	109	27	36.9	291	69	24	33.1
1948–49	1949–50	297	380	128	35.9	215	233	108	32.8
1949–50	1950–51	1,210	496	41	35.0	771	364	47	32.7
1950–51	1951–52	1,526	285	19	34.2	1,229	204	17	32.7
1951–52	1952–53	1,017	67	7	33.4	797	20	3	32.8
1952–53	1953–54	89	66	74	32.7	23	12	52	33.0
1953–54	1954–55	108	184	170	32.0	16	148	925	33.4
1954–55	1955–56	409	199	49	31.5	339	185	55	33.9
1955–56	1956–57	467	157	34	30,9	437	110	25	34.5
1956–57	1957–58	247	78	32	30.4	175	60	34	35.2
1957–58	1958–59	162	67	41	30.0	109	56	51	36.1
1958–59	1959–60	338	22	7	29.6	233	9	4	37.1
1959–60	1960–61	181	56	31	92.3	56	40	71	38.3

longer lived northern fish. As an example, the geometric mean of survival for the 7 years 1942–48 was 54 percent in the Pacific Northwest and 32 percent in San Pedro. Aside from the effects of changing population composition, effort, and availability, survival probably remained relatively unchanged over the 28-year period.

Although not measurable, the effects of availability may be seen in the increasingly large fluctuations in survival toward the end of the 28-year period in figure 25. It appears that availability has had its greatest effect on the northern periphery of the sardine range, and considerably influenced the catch in British Columbia and the Pacific Northwest throughout the existence of the fisheries in these areas. Population size, however, also exerted great influence and was undoubtedly related to availability in this area. Certainly population size was the primary factor influencing the fisheries when all ports are considered. In more recent years the reduction of the range of the sardine has caused the effects of availability to be felt much farther to the south, and the relatively larger proportion of the population affected has caused the greater fluctuation in apparent survival. In at least a few of these later years availability has probably been the dominant factor affecting the fishery, although population size and availability are probably to a certain extent themselves related. Nevertheless, over the period of years treated in this paper, population size has been, without any doubt, the primary and dominating factor influencing the success of the fishery.

SUMMARY

1. For the 26-year period (1932–1957) an excellent negative correlation exists between anomalies of spawning-stock size and year-class size for the Pacific sardine.

2. This correlation may be demonstrated by correlating deviations from trends of the two parameters or by directly correlating the parameters for three (all ports) or two (San Pedro only) periods of no no trend separated by fishery failures and a reduction in sardine range.

3. The data indicate that the good negative correlation existing between spawning-stock size and year-class size is not a secondary result of year classes occurring in cycles which generate cycles of population size several years later.

4. The indices of year-class size and spawning-stock size are based on catch, which is determined primarily by actual population size. Catch may also be influenced by fishing effort and availability. During the period of study effort seems to have been near saturation, and changes in effort had little effect on catch. On the other hand, catch appeared to have considerable effect on the amount of effort expended, especially in the two immediately following seasons, with large catches causing increased effort and small catches causing decreased effort. Availability seems to have been secondary to population size in determining catch, although the effects of availability as evidenced by apparent total mortality rates appeared to increase during the latter half of the 26-year period.

LITERATURE CITED

CLARK, FRANCES N., AND JOHN C. MARR.
1955. Part II: Population dynamics of the Pacific sardine. California Department of Fish and Game, Marine Research Committee, Progress Report California Cooperative Fisheries Investigations, 1 July 1953 to 31 March 1955, pp. 11–48.

DAUGHERTY, ANITA E., AND ROBERT S. WOLF.
1960. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1957–58. California Fish and Game, vol. 46, No. 2, pp. 189–194.

ECKLES, HOWARD H.
1954. Age composition of the commercial catch of Pacific sardines, 1932–38. *In* Kenneth H. Mosher and Howard H. Eckles, Age determination of Pacific sardines from otoliths, pp. 24–40. U.S. Fish and Wildlife Service, Research Report 37.

FELIN, FRANCES E., RAY ANAS, ANITA E. DAUGHERTY, AND LEO PINKAS.
1950. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1949–50. California Fish and Game, vol. 36, No. 3, pp. 241–249.
1951. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1950–51. California Fish and Game, vol. 37, No. 3, pp. 339–349.

FELIN, FRANCES E., JOHN MACGREGOR, ANITA E. DAUGHERTY, AND DANIEL J. MILLER.
1953. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1952–53. California Fish and Game, vol. 39, No. 3, pp. 409–417.
1954. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1953–54. California Fish and Game, vol. 40, No. 4, pp. 423–431.
1955. Age and length composition of the sardine catch off the Pacific coast of the United States and

Mexico in 1954–55. California Fish and Game, vol. 41, No. 4, pp. 285–293.

Felin, Frances E., and Julius B. Phillips.
1948. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada, 1941–42 through 1946–47. California Division Fish and Game, Fish Bulletin No. 69, 122 pp.

Felin, Frances E., Julius B. Phillips, and Anita E. Daugherty.
1949. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1948–49. California Fish and Game, vol. 35, No. 3, pp. 165–183.

Felin, Frances E., Robert S. Wolf, Anita E. Daugherty, and Daniel J. Miller.
1958. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1955–56. California Department Fish and Game, Fish Bulletin No. 106, pp. 7–12.

Herrington, William C.
1948. Limiting factors for fish populations: some theories and an example. A symposium on fish populations. Bulletin of the Bingham Oceanographic Collection, vol. XI, art. 4, pp. 229–283.

Marr, John C.
1960. The causes of major variations in the catch of the Pacific sardine, *Sardinops caerulea* (Girard). Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, vol. 3, pp. 667–791.

Mosher, Kenneth H., Frances E. Felin, and Julius B. Phillips.
1949. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1947–48. California Fish and Game, vol. 35, No. 1, pp. 15–40.

Ricker, William E.
1954. Stock and recruitment. Journal Fisheries Research Board of Canada, vol. 11, No. 5, pp. 559–623.

Wolf, Robert S.
1961. Age composition of the Pacific sardine 1932–60. U.S. Fish and Wildlife Service, Research Report 53, 36 pp.

Wolf, Robert S. and Anita E. Daugherty.
1961. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1958–59. California Fish and Game, vol. 47, No. 3, pp. 273–285.

Wolf, Robert S., John S. MacGregor, Anita E. Daugherty, and Daniel J. Miller.
1958. Age and length composition of the sardine catch off the Pacific coast of the United States and Mexico in 1956–57. California Department Fish and Game, Fish Bulletin No. 106, pp. 13–17.

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